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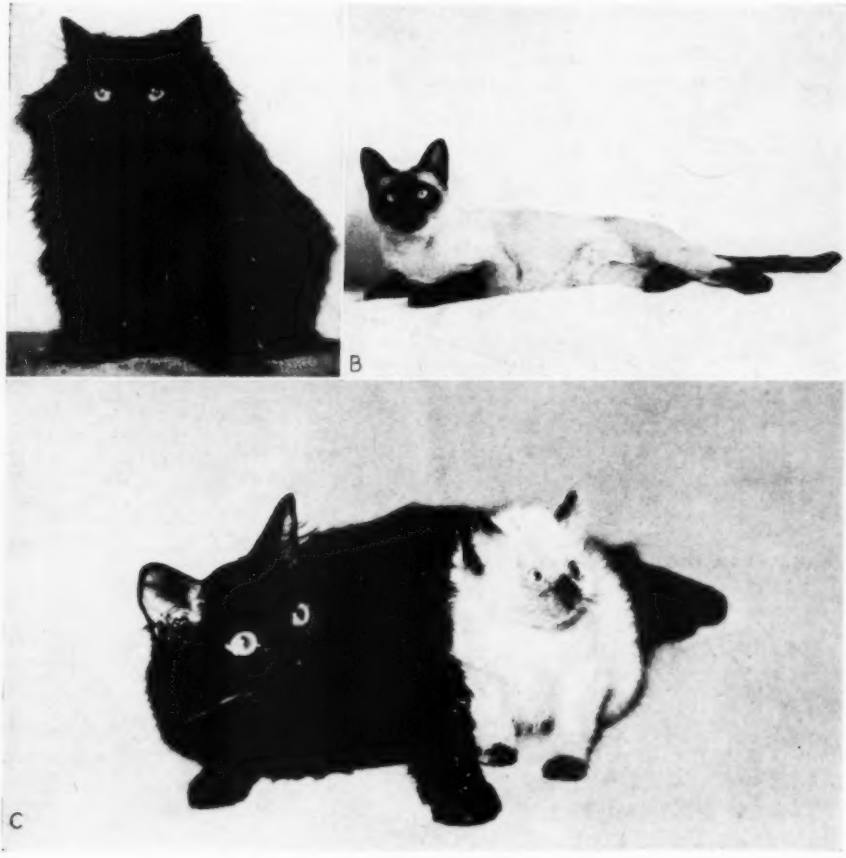

SOMETHING NEW IN KITTENS
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Genetics of the California Poppy — *Metaxenia in Apples*
A Maze-test for Twins — *Structure of Salivary Gland Chromosomes*
Long-range Paternity in Sheep — *Genetics and the Causes of Cancer*
Varietal Differences in Endocrine Glands — *How Mosaics are Made*

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STUDENT SUBSCRIPTIONS

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INHERITED DIFFERENCES IN PISTIL LENGTH

Frontispiece

The pistil of the California poppy flower usually does not extend beyond the stamens, as is shown at the left. (Part of the stamens have been removed to show the pistil.) At the right is shown a variation in which the pistil extends far beyond the anthers. This character is inherited as a mendelian dominant. Approximately 15 ×.

GENETIC STUDIES ON THE CALIFORNIA POPPY

A. V. BEATTY*
The Blandy Experimental Farm, University of Virginia

A GENETICAL study of the California poppy, *Eschscholzia californica,* was begun in 1932 and is still in progress. The following account is preliminary to a more extensive study which it is hoped will be presented later.

The genus *Eschscholzia,* which belongs to the Papaveraceae, has, according to the Index Kewensis, 124 accepted species. There exists a general opinion that the actual number of good species is far less than 124, and that the majority of described species are varietal forms of *Eschscholzia californica.* For this reason it was thought that a genetical study of this species would supply a simple means for straightening out the taxonomy of the genus.

Fifty commercial varieties have been examined during the course of this investigation. Since the material was obtained from several different sources, a number of characters, particularly the flower colors, were frequently duplicated. It has not been possible to continue all of these lines because of the prevalence of self-sterility in this species, but the characters studied have been maintained in self-fertile races for further study.

Even though most of the plants were self-sterile, every flower was emasculated before crossing. The removal of the stamens, in most cases, was accomplished by gently removing the petals, although in some varieties only the outer row of stamens seemed to be attached to the petals, so that it was necessary to extract the remaining stamens with a pair of forceps. The anthers usually do not dehisce until after the flower opens. The stigmas, however, are receptive before the flower opens, and remain so from eight to ten days if fertilization does not take place. If fertilization is accomplished the stigmas wither within two or three days.

Each individual flower used in the experiments was covered with a cellophane bag. The bags were obtained from a Woolworth chain store, where they are used for wrapping tooth brushes. They are made of thin material and, when inflated, are 20 mm. in diameter and 90 mm. in length. Two small openings, about 5 mm. in diameter, were made in the top and covered by a wad of cotton placed in the end of the bag. This provided a means for controlling the moisture content within the bag.

A discussion and a brief description of each of the characters investigated follow.

Flower Colors

The corolla colorations were of four types, namely: red, orange, and two ground colors, white and yellow, which produced the color of the flower in the absence of red and orange. All coloring material was found in the epidermal layers.

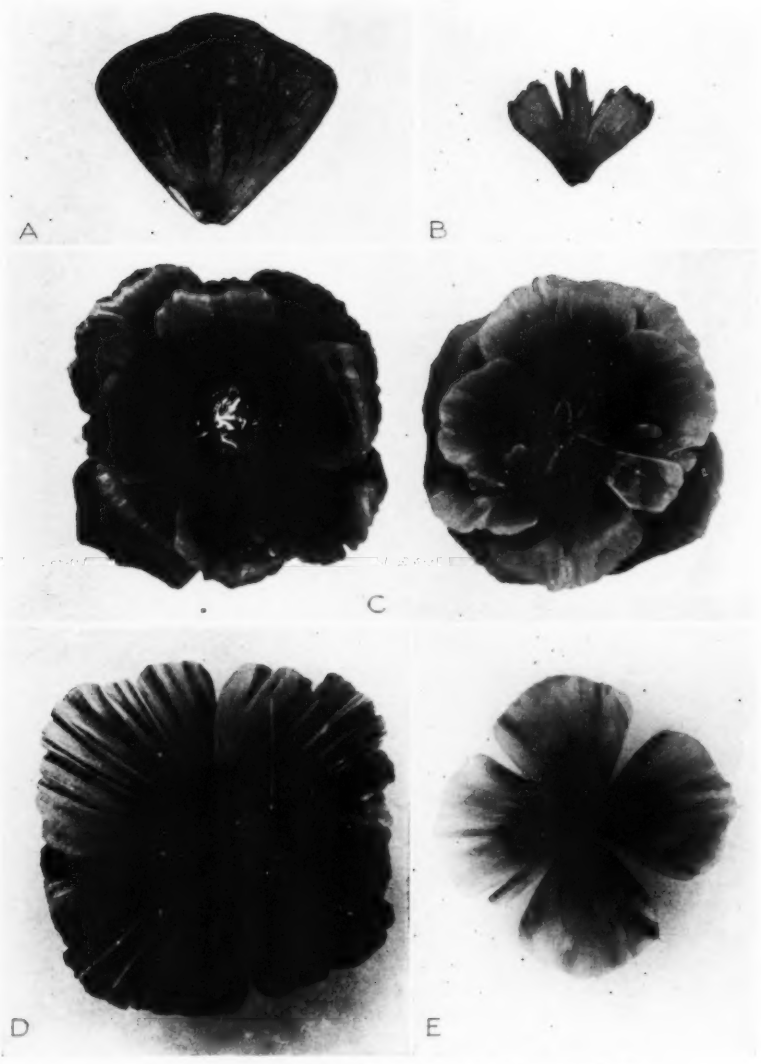
Yellow (*CC*) and white (*cc*) form an allelic pair—yellow being dominant to white. Thirty-six crosses were made involving these colors and the summation of the F_2 results is given in Table I.

TABLE I

F_2 families, Yellow (*CC*) × White (*cc*)

36 families	Yellow	White
Actual ratio	3580	1131
Theoretical (3:1) ratio	3533	1178

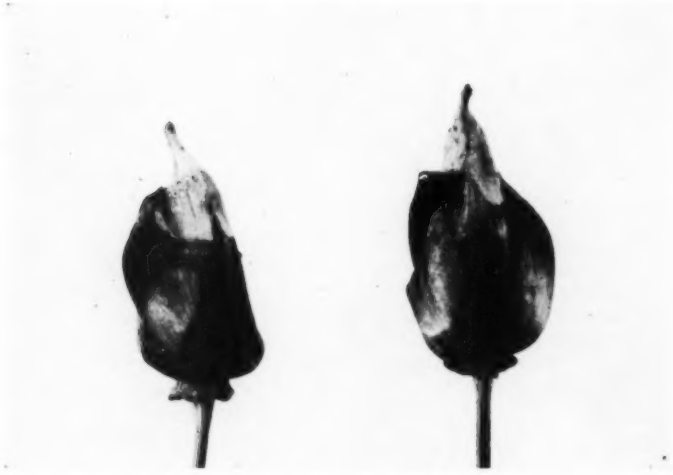
*The writer wishes to express his appreciation to Dr. Orland E. White for the helpful suggestions and criticisms given during this investigation, and to Mr. Robert C. Cook for photographing the material.



INHERITED VARIATIONS IN FLORAL STRUCTURE

Figure 1

Striped flowers (*A*) are conditioned by a dominant gene, *Si*. The fringed variation (*B*) is a simple recessive to normal development of the petal. Doubleness is a variable character apparently conditioned by a main gene and possibly several modifiers. The two flowers shown here (*C*) may be classed as intermediate doubles, the maximum number of petals in double flowers being 14. The pleated variation (*D*) is a dominant to the normal petal form. The flower at (*E*) shows the type of spotting almost universerly observed in this species. The size of the spot varies greatly, this specimen having a medium orange spot on a yellow petal. This flower also shows the normal allels of the characters illustrated, being non-striped, non-pleated, non-fringed, and single.



A SELF FERTILIZING ADAPTATION

Figure 2

In one F_2 family the calyces remained adherent to the tips of the flowers, preventing their opening, thus assuring self-fertilization of the flowers. A method similar in principle was published some years ago for self-fertilizing cotton by placing a rubber band around the bud. Here the poppy seems to have gone the plant breeder one better by taking care of the job itself! The inheritance of this character is undetermined, though its appearance in one F_2 family strongly suggests that one or more recessive factors are involved.

Associated with the yellow color was a basal orange blotch (Figure 1*E*) similar in shape and position to that common in other members of the Papaveraceae. In only one case was the yellow color found without the blotch, and this plant was both self- and cross-sterile. Uphof[6] reported that in a related species, *Eschscholzia mexicana,* he found yellow flowers with and without an orange base, and that when the two were crossed the orange base was dominant and gave a monohybrid ratio.

The orange and red colors may appear individually or in combination on either ground color. The flower color produced depends (1) upon the ground color, (2) upon the presence of red, orange, or both, and (3) upon the action of modifiers.

The factors producing orange flowers have not been successfully isolated. Twenty crosses were made with orange flowers. Most of the F_1 progenies of these crosses contained numerous segregates. In the progenies that appeared to be uniform, the F_2 ratios were so variable that no factorial interpretation could be made.

Fifty-nine crosses were made between red and non-red flowers. Red flower (*RR*) was found to be dominant to non-red flower (*rr*), and gave a monohybrid ratio in the second generation (Table II).

TABLE II

F_2 families, Red (*RR*) × Non-red (*rr*)

59 families	Red	Non-red
Actual ratio	5523	1771
Theoretical (3:1) ratio	5470.50	1823.50

This factor appeared to supply the basic red color on which a number of modifiers acted, and of those four were studied.

Two factors produced a striping effect of the anthocyanin colors. One factor affected the inside of the flower,

while the other produced a similar affect on the outside of the flower. The latter was found to be recessive, but was not further analyzed.

The stripes produced by these factors are discontinuous, that is, made up of a linear series of unequal flecks. There was a great amount of variation in the expression of the factors from plant to plant and in many cases in the petals of an individual flower.

Five crosses were made between flowers striped on the inside (Figure 1*A*) and flowers non-striped. Striping (*SiSi*) is dominant to the non-striped condition (*sisi*) (Table III).

TABLE III

F_2 families, Striped inside (*SiSi*) × Non-striped inside (*sisi*)

5 families	Striped in	Non-striped in
Actual ratio	408	123
Theoretical (3:1) ratio	398	133

The other two factors inhibited the anthocyanin color on the inside of the flower. They were found to be duplicate factors. The color over the entire flower ($I_1I_1I_2I_2$) is dominant to the inhibited effect which is only expressed when the factors are in the homozygous double recessive condition ($i_1i_1i_2i_2$) (Table IV).

TABLE IV

F_2 families, Red Inside ($I_1I_1I_2I_2$) × Non-red Inside ($i_1i_1i_2i_2$)

3 families	Red inside	Non-red inside
Actual ratio	220	17
Theoretical (15:1) ratio	222	15

Floral Characters

In a commercial variety called "Fringed Yellow" a factor was isolated which produced a fringing of the petals (Figure 1*B*). There was great variation in the length of the fringes in the different plants, but when all types were considered together, fringing (*ff*) was found to be recessive to normal or entire petals (*FF*) (Table V).

TABLE V

F_2 families, Entire (*FF*) × Fringed (*ff*)

16 families	Entire	Fringed
Actual ratio	2364	709
Theoretical (3:1) ratio	2305	768

A factor was studied which produced pleated flowers (Figure 1*D*). Four crosses were made between pleated and non-pleated flowers. In the F_1 both plain and pleated flowers were found. Some of the non-pleated ones were selfed, and they gave in the next generation all plain-petaled plants. The pleated plants, when selfed, gave an F_2 ratio of 2 pleated to 1 plain indicating that pleated flower was dominant to plain flower (*pp*), but lethal when in the homozygous dominant condition (Table VI).

TABLE VI

F_2 families, Pleated (*Pp*) × Non-pleated (*pp*)

4 families	Pleated	Non-pleated
Actual ratio	256	153
Theoretical (2:1) ratio	273	136

Another petal peculiarity is called cupped. In this type the petals do not flatten out, but remain hemispherical. The side margins of the petals are in contact with each other so that they give the impression that each is supporting the other. A number of crosses were made involving this character, but in only one F_2 family was the distinction between cupped and normal petals sufficiently sharp so that the character cupped could be scored accurately. Cupped (*nn*) is recessive to normal petals (*NN*) (Table VII).

TABLE VII

F_2 family, Non-cupped (*NN*) × Cupped (*nn*)

1 family	Non-cupped	Cupped
Actual ratio	29	11
Theoretical (3:1) ratio	30	10

The anthers exhibit a variety of colors similar to the petal colors. Only one plant was found in which the anthers were entirely red, and in this plant the anthers were all slightly petaloid. All anther colors studied, except one case to be described, were self-colored. In this particular case an anthocyanin pigment was present on the inner face of the anthers. The width of the tissue containing the pigment varied considerably, but it usually consisted of a narrow strip in the center region. Four crosses were made between red-faced and non-red-faced

anthers. Red anther (*aa*) is recessive to non-red anther (*AA*) (Table VIII).

TABLE VIII

F_2 families, Non-red-faced (*AA*) × Red-faced Anthers (*aa*)

4 families	Non-red-faced	Red-faced
Actual ratio	358	116
Theoretical (3:1) ratio	355.50	118.50

One factor was found which affected the length of the pistil. Ordinarily at the time the calyx is shed and the flower begins to open the apex of the pistil is at the same height level as the anthers. Factor *L* produces long pistils in which the apex extends much beyond the tips of the anthers (Frontispiece). Associated with the elongation of the pistil is a shortening of the filamentous stigmas. The F_2's of the five crosses made between these characters indicate a one factor difference, long pistil being dominant (Table IX).

TABLE IX

F_2 families, Long Pistil (*LL*) × Normal Pistil (*ll*)

5 families	Long pistil	Normal pistil
Actual ratio	436	194
Theoretical (3:1) ratio	472.50	157.50

A number of double-flowered races have been studied. The petal number of the double flowers ranged from 5 to 14. Figure 1*C* shows two typical double flowers. Thirteen crosses were made between single flowers (4 petals) and double flowers. The F_1 plants were all single-flowered. Within five of the F_1 progenies some plants were found which produced, besides the single flower, a few flowers which had from one to four petaloid stamens. In most cases the petalody was only partial, and in many cases good pollen was produced on the petaloid structures.

In the F_2 generation there was no sharp segregation, but a continuous series from singles (4 petals) to doubles (14 petals). The petal number varied considerably in the flowers of an individual plant. When the F_2 data were statistically analyzed, singleness (*DD*) was found to be dominant to doubleness (*dd*) (Table X). Since the doubling was associated with petalody of the stamens, a statistical study was made between the petal number and the stamen number. The results of this investigation will be published later.

TABLE X

F_2 families, Single Flowers (*DD*) × Double Flowers (*dd*)

13 families	Single	Double
Actual ratio	420	200
Theoretical (3:1) ratio	465	155

Self-Sterility

The peculiar type of self-sterility exhibited by the California poppy has been of interest to many investigators. Müller[4] reported that the plants grown by him in Brazil were self-sterile. At the same time Darwin reported that he had a self-fertile race growing in England. After exchanging samples of seeds, Müller found that Darwin's fertile race, when grown in Brazil, was only partially self-fertile, while Darwin found that the self-sterile race of Müller's, when grown in England, was partially self-fertile.

Hildebrand,[3] who was also working on self-sterility in this species, reported that when flowers were selfed the average number of seeds per capsule was 6, when flowers on the same plant were crossed, the average number was 9, but when flowers from different plants were crossed, the average number was 84.

Darwin[2] reported on the comparative viability of plants obtained from seeds resulting from self- and cross-fertilization. With a few exceptions there was no difference in viability, but the plants derived from seeds of a cross were much more productive in both the number of flowers and the number of seeds per capsule.

Stout[5] found most of the plants of the California poppy grown by him were self-sterile. In the few that were self-fertile, except in one case, the fertility was feeble. He concluded that the incompatibility operated after fertilization because a number of self-sterile plants produced small capsules which contained a number of shriveled seeds.

INHERITED DIFFERENCES IN GROWTH HABIT

Figure 3

Three factors affecting the growth habits of the plants were studied. These were erect growth habit (*A, B*), basal leaves (*B*), and procumbent (*C*). The erect type (*B*) is dominant over the procumbent type (*C*). The basal leaf variation (*B*) is dominant to the non-basal leaf form (*A*). Usually the basal leaf habit was associated with erect growth.

In general all of the varieties studied by the writer were self-sterile. In three cases, however, plants which were tested throughout the summer and found to be self-sterile produced one capsule each which contained a few (less than ten) good seeds. The seeds from such plants were slow to germinate, and all of the plants died before flowering.

In every variety at least one plant was found which was self-fertile. The number of seeds per capsule produced from these plants ranged from 1 to 100. (For a comparison in the number of seeds, the maximum number found in any one capsule was 150. This capsule resulted from a cross.) The seeds from these self-fertile plants germinated only slightly more slowly than seeds obtained from crosses. From about 5,000 seeds obtained from these selfed flowers approximately 25% germinated, but only ten lived long enough to flower. Seven of those died after producing two or three flowers, and the remaining three, each from a different variety, were self-sterile.

Eight crosses were made between these self-fertile and self-sterile plants. All of the F_1's were fertile, and the F_2 plants segregated in a ratio of 3 fertile to 1 sterile (Table XI). The type of self-fertility found in the F_2 plants was only partial and not complete as was exhibited in some cases by the one parent. The number of seeds per capsule in these F_2 fertile plants ranged from 1 to 20.

TABLE XI

F_2 families, Fertile *(SS)* × Sterile *(ss)*

8 families	Fertile	Sterile
Actual ratio	347	139
Theoretical (3:1) ratio	364.50	121.50

This factor for self-sterility operates by inhibiting the growth of the pollen tubes. Since there are four or more filamentous stigmas to a flower, it was possible to place pollen from a flower of another plant on some of the stigmas and pollen from the flower itself on the remaining ones. In all cases both types of pollen germinated equally well, but soon after germination growth was inhibited in the pollen taken from the same flower used in the experiment. Likewise if a fluid extracted from several stigmas of a plant was placed on an artificial culture (Beatty[1]) of pollen from the same plant, the growth of the pollen tubes was inhibited.

In several cases an individual flower was both selfed and crossed with a flower from another plant in order to determine whether the germination and growth of the foreign pollen would affect the growth of the pollen from the same flower used in the experiment. The character *fringed* was used to mark the plants resulting from self-fertilization, and the character *red flower* was used to mark the plants resulting from a cross. The results were negative in that all the progeny had red flowers.

In one F_2 family a peculiar character was found in which the calyx was not entirely shed, but remained attached to the apical end of the petals (Figure 2), and caused the flowers to be self-fertilized. The inheritance of this character remains undetermined.

Foliage Characters

The foliage characters studied were all found to be greatly influenced by environmental conditions. Some characters which were quite distinct in the parents blended into one another in the F_2 generation so that it was not possible to record them. Of the ones studied, glaucous foliage was the sharpest and most easily scored. This type is characterized by having a glaucous covering on the stems and leaves. The covering can be easily brushed off and for this reason older plants are less glaucous. A single factor difference exists between glaucous (*GG*) and non-glaucous foliage (*gg*) (Table XII).

TABLE XII

F_2 families, Glaucous *(GG)* × Non-glaucous *(gg)*

8 families	Glaucous	Non-glaucous
Actual ratio	696	250
Theoretical (3:1) ratio	709.50	236.50

The types of branching were particu-

larly susceptible to the environment. An erect and procumbent type were most easily studied due to the fact that the erect type usually had one or two main stems, while the procumbent type had several (Figure 3). The erect type (*EE*) is dominant to the procumbent type (*ee*) (Table XIII).

TABLE XIII

F_2 family, Erect (*EE*) × Procumbent (*ee*)

1 family	Erect	Procumbent
Actual ratio	104	40
Theoretical (3:1) ratio	108	36

A rosette of basal leaves was usually associated with the erect type of branching. Basal leaves (*HH*) was found to be dominant to the non-basal-leaved condition (*hh*), and gave a monohybrid ratio in the second generation (Table XIV). Figure 3*B*.)

TABLE XIV

F_2 family, Basal (*HH*) × Non-basal Leaves (*hh*)

1 family	Basal	Non-basal
Actual ratio	108	36
Theoretical (3:1) ratio	108	36

The stems of some of the varieties were striped with an anthocyanin pigment. The stripes were most apparent on the main stems. The presence of an anthocyanin pigment at the base of the stem, a character entirely independent, made scoring in many cases very difficult. Red-striped stem is produced by duplicate factors and is dominant ($T_1T_1T_2T_2$) to non-red stems ($t_1t_1t_2t_2$) (Table XV).

TABLE XV

F_2 families, Red-striped ($T_1T_1T_2T_2$) × Non-red-striped ($t_1t_1t_2t_2$)

3 families	Red-striped	Non-red striped
Actual ratio	437	75
Theoretical (15:1) ratio	480	32

Summary

The flower colors studied in the California poppy can be placed into four groups: orange, red, yellow, and white. Yellow and white are ground colors and produce the color of the flower in the absence of red and orange.

Twelve factor pairs gave 3:1 ratios: *CC—cc*, yellow—white flower; *RR—rr*, red—non-red flower; *SiSi—sisi*, striping of anthocyanin color on inside of flower—non-striped; *FF—ff*, non-fringed—fringed flower; *NN—nn*, non-cupped—cupped flower; *AA—aa*, non-red-faced—red-faced anthers; *LL—ll*, long—normal pistil; *DD—dd*, single—double flower; *SS—ss*, self-fertility—self-sterility; *GG—gg*, glaucous—non-glaucous foliage; *EE—ee*, erect—procumbent branching; and *HH—hh*, basal—non-basal leaves.

One factor pair gave a 2:1 ratio: *Pp—pp*, pleated—non-pleated flower.

Four factor pairs involved two sets of duplicate factors and gave 15:1 ratios: $I_1I_1I_2I_2$—$i_1i_1i_2i_2$, non-inhibiting—inhibiting anthocyanin color on inside of flower; and $T_1T_1T_2T_2$—$t_1t_1t_2t_2$, red-striped stem—non-red-striped stem.

Flower doubling is associated with petalody of the stamens. In the second generation of a cross single flower (4 petals) × double (14 petals) no sharp segregation occurred, but a continuous series existed from singles to doubles with 14 petals.

The type of self-sterility studied was caused by an inhibition of the growth of the pollen tubes.

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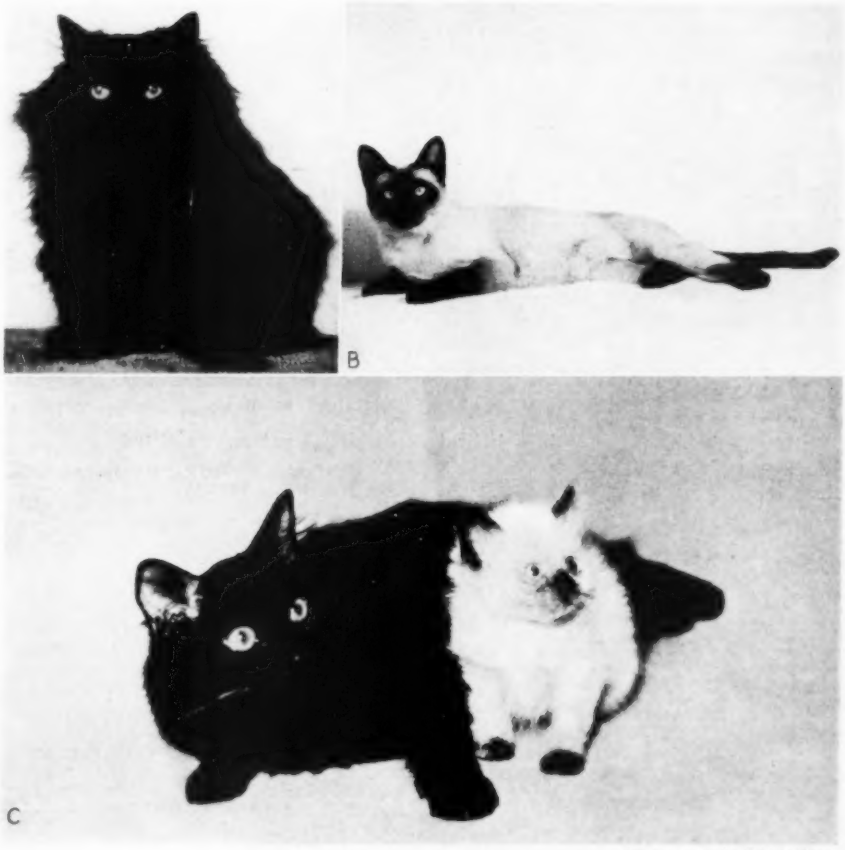
SIAMESE-PERSIAN CATS

CLYDE E. KEELER and VIRGINIA COBB
Howe Laboratory, Harvard Medical School, and the Siamese Cat Society of America



Photographs by Edwin Gray

SOMETHING NEW IN KITTENS

Figure 4

The startled, black-nosed youngster (*C*) represents a successful attempt to apply genetics to combining the characteristics of Persian and Siamese cats. This kitten, having the long hair of the Persian and the markings of the Siamese, is a true-breeding form which may represent the origin of a new breed. He was produced by mating Persian (*A*) with Siamese (*B*). The first generation were black and short-haired. Among the progeny produced by mating together these short-haired, black individuals, one in fifteen should show the Persian-Siamese combination. Since the long hair of the Persian and the pattern of the Siamese are both simple recessive characters, the combination of them is expected to be true breeding.

IN 1931 we decided that there would be a place in the cat fancy for a new breed combining the color pattern of the Siamese with the hair length and other qualities of the Persian. We realized that from the fancier's point of view it was desirable to employ only pedigreed animals of both breeds contributing

to the foundation stock for the projected Siamese-Persian breed.

According to our previous analysis[1] of long hair and Siamese, both characters behave in the heredity of the cat as simple recessive Mendelizing unit-characters. Therefore, barring the possibility of linkage, the problem would be one simply of crossing together non tabby individuals of the two breeds and of raising enough kittens in the F_2 generation to procure the desired combination.

In the spring of 1931 a pedigreed Siamese female was mated to a pedigreed black Persian male. As a result of this mating there was produced a litter of three black short hair male kittens.

The following year a pedigreed black Persian female (Figure 4*A*) was mated to a pedigreed Siamese male (Figure 4*B*) and from the resultant litter of black short hair kittens (1 male and 1 female) a female was reared.

In 1933 the black short hair hybrid female was mated to one of the black short hair hybrid males and a litter was produced which contained a black long hair female (Figure 4*C*). From this cross, with free segregation of two recessive Mendelizing characters (long hair and Siamese) we would expect a ratio of 9 short hair black, 3 Siamese, 3 long hair black and 1 Siamese-Persian.

The black long hair female proved by genetic test to be heterozygous for Siamese color, and when mated to her black short hair father in 1935, produced two Siamese-Persians, one of which is shown in Figure 4*C*.

This year the same mating was repeated, and this resulted in another Siamese-Persian. From this mating we expect a ratio of 3 black short hair, 3 black long hair, 3 Siamese (short hair), 1 Siamese-Persian.

So far as we are aware these three kittens are the first Siamese-Persians to be scientifically synthesized from pedigreed foundation animals.

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Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the* JOURNAL *will be reviewed in later numbers.

THE VARIATION OF ANIMALS IN NATURE, *by* G. C. Robson, M.A., Deputy Keeper of Zoology, British Museum, and O. W. Richards, M.A., D.Sc., Lecturer in Entomology, Imperial College of Science and Technology. With 2 Colored Plates and 30 Illustrations in the Text. Pp. 425. Price, $8.25. London, Toronto, and New York: Longmans, Green and Co., 1936.

WORLD IMMIGRATION, With Special Reference to the United States, *by* Maurice R. Davie, Professor of Sociology in Yale University. Pp. 588. Price, $3.75. New York: The Macmillan Co., 1936.

PROSTITUTION, An Investigation of Its Causes, Especially with Regard to Hereditary Factors, *by* Tage Kemp. Pp. 253. Copenhagen: Levin & Munksgaard; London: William Heinemann (Medical Books) Ltd., 1936.

TRAIL BLAZERS OF SCIENCE, Life Stories of Some Half-Forgotten Pioneers of Modern Research, *by* Martin Gumpert, translated from the German by Edwin L. Shuman. Pp. 306. Price, $2.50. New York and London: Funk & Wagnalls Co., 1936.

KONSTITUTIONSFORSCHUNG UND KRANKHEITSBEKAMPFUNG IN DER TIERZUCHT, by Dr. med. vet. habil W. Schaper. Pp. 88. Berlin: Verlag von Paul Parey. 1936.

ELEMENTS OF PSYCHOLOGY, *by* Knight Dunlap, Professor of Psychology in the University of California at Los Angeles; formerly Professor of Experimental Psychology in the Johns Hopkins University. 65 illustrations. Pp. 499. Price, $3.00. St. Louis: The C. V. Mosby Co., 1936.

FREEDOM AND RESPONSIBILITY, A Biological View of Some Problems of Democracy, *by* Edwin Grant Conklin, Princeton University. Pp. 88. Price, $1.00. Boston and New York: Houghton Mifflin Co., 1935.

AN EXPERIMENT IN EUTELEGENESIS*

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THE possibility of impregnating a female mammal by injection of semen into the uterus or vagina by means of instruments, without there being any actual intercourse with a male, was first demonstrated under scientifically controlled conditions by Spallanzani in 1780. Since that date the method has been tried in both human and veterinary practice as a means of overcoming certain forms of sterility, and in many cases successful results have been obtained.

By many of the earlier experimenters the possibility of extending the method to practical livestock improvement was suggested and experiments both in America and Europe were initiated in this direction. Among the pioneers in this field were Professor Ivanov and his co-worker, Dr. Wróblewski, who made extensive experiments in Russia. The possibility of preserving the semen at a low temperature and transmitting it to a distance was one of his objectives, as indicated in his important monograph,[6] in which he describes removing the testicles from a bull slaughtered at the abattoir and with the sperm inseminating two cows at the School of Agriculture. In 1926 he succeeded in keeping spermatozoa in a fertile condition in the excised epididymis of the Guinea pig for 4-6 days and obtained offspring as a result of insemination with this material.[7] Contemporaneously with these experiments Hammond[4] and Walton[15] worked out the optimal conditions for survival of fertility of rabbit spermatozoa *in vitro* and obtained a maximal survival of about seven days. In July, 1926, spermatozoa of the rabbit were sent packed in ice in a thermos flask from Cambridge to Edinburgh through the ordinary post and successful inseminations were made.[14]

In the meantime artificial insemination for practical livestock improvement has been developed on a large scale in Soviet Russia. The scientific direction of this work is centered at the Laboratory of Artificial Insemination, Institute of Animal Husbandry, Lenin Academy of Agriculture, Moscow. Millions of cattle, sheep and horses are inseminated annually on the collective and state farms in the U.S.S.R. Experiments on the transport of semen to a distance have also been carried out, using a similar method of transport to that adopted in the Cambridge experiment described above. An international exchange of ram semen between Moscow and Cambridge was attempted in September, 1935, but broke down owing to customs and other difficulties. The expedition of ram semen to Poland however has been successful and is of interest as being the first successful attempt to send semen from one country to another by ordinary commercial air mail.

Fathering "the Airman"

A description of the modern technique of artificial insemination will be found in the references marked with an asterisk in the bibliography. In this

*For much help in this experiment we are indebted to Dr. J. Hammond and Messrs. Tadman, Andrews, and Swan of the Animal Research Station, Cambridge, and to Dr. Z. Zabielski and ing. agr. M. Borowska of the Zootechnical Station, Borowina, National Institute for Agricultural Research, Pulawy, Poland. The Polish photographs are published by courtesy of Dr. Laura Kaufmann and Dr. Latyszewski.

LOTNICK, THE SUFFOLK × POLISH "AIR MAIL" LAMB

SUFFOLK SUFFOLK × POLISH POLISH

LONG RANGE PATERNITY

Figure 5

The cross-bred Suffolk × Polish lamb "Lotnick" is, as far as published record shows, the first mammal to be sired by international air mail. His father was a Suffolk ram, at the Cambridge Experimental Farm in England, and his mother (upper right) was a Polish ewe, at the Zoological Institute at Borowina, Poland. Neither parent strayed from home, but through the agency of modern knowledge regarding artificial insemination and the air mail, "Lotnick" (Polish for "Airman") was born at the Polish Zoological Institute on April 28, 1936. Below is shown the genetic evidence that "Lotnick" really owes his paternity to modern biology and transportation, and not to a Polish sire nearer at hand. The pure Suffolk lamb has a colored fleece and a black face. The pure Polish has a white fleece and a white face. Lotnick combined the face color of one parent with the fleece color of the other. This combination regularly appears in the cross, and proves his hybrid ancestry.

particular experiment semen was collected from a Suffolk ram (No. 47) by means of the "artificial vagina" technique at 4 p. m. on December 5th, 1935, at the Animal Research Station, Cambridge. Two samples, each consisting of about 0.75 ml. of dense active sperm, were obtained and immediately transferred to narrow "Pyrex" test tubes (5 mm. diameter). The space above the sperm in the tube was filled with medicinal paraffin (paraffinum liquidum B.P.) and the tube corked. Each tube was wrapped in cotton-wool and the whole covered with a thin rubber finger stool tied tightly at the open end. This wrapping prevents the sperm in the tube from sudden change in temperature, which has been found to be inimical to survival. The rubber stool prevents the cotton-wool from becoming wet; it is preferable to glass as a sudden jar will not break it. The wrapped tubes were first placed in a Thermos flask containing water at 10° C. for one hour. After this preliminary pre-cooling the tubes were transferred to a hard glass thermos flask, of 1 pint capacity, containing chipped ice. The flask was then packed in a thick roll of corrugated cardboard and dispatched by the ordinary commercial Air Mail Service to Warsaw. At Warsaw the aeroplane was met and the package taken to the Zootechnical Institute at Borowina, Pulawy. The tubes were removed from the package at 7 p. m. on December 7th (two days, three hours after collection). After allowing the tubes to stand for a little time to acquire gradually the temperature of the room the semen was examined microscopically and showed good activity. It was then diluted and five ewes of the local Polish breed which were known to be "on heat" were inseminated. Every precaution was taken to keep the ewes apart from males so that the parentage of the offspring would be beyond dispute.

In due course two ewes proved to be in lamb. One ewe unfortunately aborted before term; the other produced a ram lamb on April 28, 1936. Even at birth the male parentage was evident from the pigmentation on the head and legs, the length of the tail, and the closeness of the wool. The photographs show the distinctions clearly. The cross-bred lamb which was appropriately called "Lotnik" (The Airman) is shown alongside a lamb of pure Polish breed somewhat older, while a pure Suffolk lamb is shown in an accompanying photograph.

The experiment is to be regarded as preliminary; it will be repeated on a larger scale next season. With more experience with the technique a higher percentage of successful inseminations will no doubt be achieved. Other experiments have shown that semen can be kept for even longer periods; in fact the pure Suffolk lamb shown in the photograph was produced with sperm kept for four days before insemination.

Practical Uses

From a commercial standpoint artificial insemination offers considerable possibilities. By using dilutors a single ejaculation of a ram can be used to inseminate 30-40 ewes. This means that the number of offspring obtainable from a single male of superior quality can be increased enormously. It is limited practically by the number of ewes available, but with organization this number may be very great. For example in Soviet Russia under State Management and collectivization 2,700 ewes have been inseminated with sperm from one ram in one breeding season. The advantages to be gained are, firstly, an economy in the number of rams required and secondly, the possibility of using almost exclusively the very best males.

Similar methods are applicable to the other domesticated animals, but so far with not quite so satisfactory results. Bull sperm has been kept for three days, but with diminished fertilizing capacity. Transport is, however, possible over short distances. Horse sperm can be kept for about six hours but this does not allow a wide range of distribution. Under laboratory conditions

semen of the horse has been kept for 24 hours. Boar sperm can only be kept a few hours and as yet no attempt at transportation has been made. There is, however, every prospect that in the near future the technique of storage will be improved and the transport of semen of all the domesticated animals made feasible in commercial husbandry. Possible applications to humans have been adumbrated by Brewer[1], who coins the useful word "Eutelegenesis," and by Muller[10].

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Seventh Genetics Congress to Have General Eugenics Section

THE Organization Committee of the Seventh International Genetics Congress, to be held next summer in Moscow, has decided to hold a special general session entitled "Human Genetics and Race Theories." It is understood that speakers at this session will be free to touch on questions concerning not only human genetics but of eugenics as well. The desirability of such a session was urged on the Organization Committee by a group of American geneticists in a circular letter forwarded in the spring. This session should be most illuminating and should help to clarify the troubled question of genetics and politics which has been the subject of several recent communications to the Journal.

An inquiry was addressed to the Committee early in the summer regarding transportation plans. It was pointed out that many Americans who wish to attend the Congress must await rather detailed information regarding the time and money involved in the trip to Moscow before a final decision can be made. With the Congress only eleven months away it is to be hoped that an announcement regarding transportation will not be long delayed.

METAXENIA IN APPLES*

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METAXENIA is the term used by plant workers to describe any phenomenon that may be caused by the action of the zygote upon the surrounding maternal tissue. The term was suggested by Swingle[14] to describe his observation that the maturity of dates can be made to vary with time according to the pollen which is used in fertilization.

The basic phenomenon has received attention also by investigators of vertebrate physiology, where "metaxenia" immediately suggests the influence of the fetus on the maternal organism during gestation. Metaxenia in animals is necessarily only analogous to that in plants because the mechanism by which it is brought about is different in plants and animals.†

In the animal kingdom (rabbits) it has been found that the placenta does not pass from the fetus to the mother such materials as insulin, adrenalin, pituitrin[4] or parathyroid[5] while phenolsulphonphthalein injected into the fetus is recovered in the maternal urine.[7] The substance phenolsulphonphthalein passes from the zygote to the maternal system, but in the case of this dye a foreign substance is observed which has nothing to do with the paternal origin of the embryo and hence does not belong under the heading metaxenia. In the case of diabetic mothers metaxenial effect is observed inasmuch as the child may help the mother burn her sugars. This effect, although indirect, may indicate one mode of reaction of the zygote on the maternal organism.

Metaxenia is a genetical problem and, like all genetical phenomena, expresses itself through physiological means. While the problem itself is simple, the mode of its expression becomes so complex that it may obscure the problem. In higher plants the formation of a zygote helps to liberate growth hormones which cause those parts of the fruit outside of the embryo and endosperm to grow. These growth hormones, while not individually specific in quality, may be influenced by the individual parent in quantity or in rate of action. This is illustrated in the case of Swingle's dates where the "father" is observed to change the speed of the development of the tissue surrounding the zygote.

Early Observations

In the apple observations on metaxenia antedate the discovery of the mechanism of fertilization in plants. In 1739 Bradley (see Turner[15]) described metaxenia "of the Codlin with a Pearmain, which will occasion the Codlin so impregnated to last a longer time than usual and be of sharper taste." Turner himself observed metaxenia in the Codlin, Ribston Pippin, Holland Pippin and White Winter Calville. Darwin[3] devotes six pages to "the direct or immediate action of the male element on the mother form" and refers to several cases of metaxenia in apples. In more recent years metaxenia has again been tested. Most investigators have been interested in size and shape of crop, some also in chem-

*Approved by the Director of the N. Y. State Agricultural Experiment Station for publication as Journal Paper No. 152, June 25, 1936.

†As the word signifies, metaxenia is grammatically a plural form but perhaps we may be justified to use it as a singular as long as we are reminded that the term may describe a variety of observations under the same heading.

ical composition. Reports that definite paternal characters such as ribbed fruit or color could be transmitted as metaxenia have not been substantiated by the more careful investigators.

Most workers have taken great care to distribute the experimental apples evenly over the bearing surface of a single tree and Krumbholz[6] went so far as to equalize the number of leaves per fruit to avoid systematic errors. Metaxenial results have thus not usually been obscured by differential effects of nutrition.

In discussing metaxenia in apples and pears it is often argued that any differences observed between two groups of apples or pears are the result of a difference in seed number. Brittain[1] using nearly 6,000 apples from 6 controlled pollinations found a correlation of 0.3 between seed number and apple size in only two of the six combinations studied. In the other four combinations the correlation was even less. In contrast, positive correlations between seed number and apple size were found by Nebel and Kertesz.[13] Metaxenia should therefore be tested in crosses of similar fertility otherwise allowance for this factor should be made.[13]

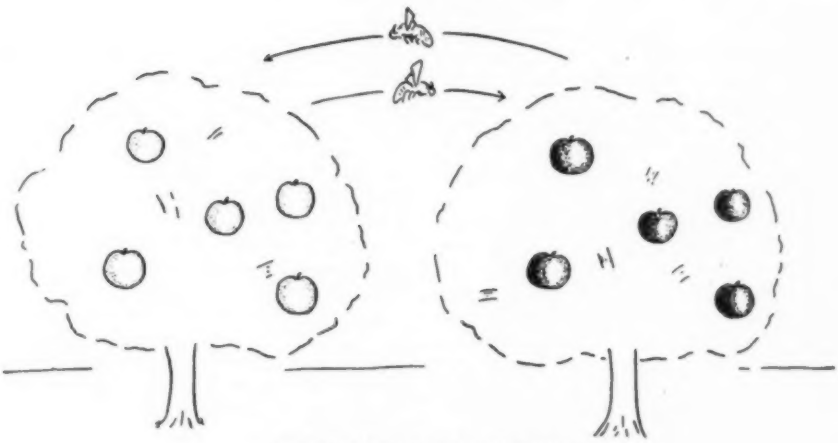
Lewis and Vincent[8] reported increases in average weight of 9 per cent and 15 per cent respectively in the crosses Yellow Newtown × Jonathan and Yellow Newtown × Grimes Golden compared with Yellow Newtown × Spitzenburg. In these combinations the heaviest combination showed the lowest average seed number. Crow[2] showed metaxenia increasing the weight of Wealthy apples when crossed with McIntosh as compared with the combination Wealthy × Wagner. Here again average seed number in the two groups varied inversely to apple size.

Krumbholz[6] found that the variety Baumann's Reinette used as a male parent consistently produced larger apples than most other varieties with which it was compared as a male. Seed numbers in these combinations were equal and frequently inversely related to size of crop. Krumbholz pointed out the important fact that metaxenial differences could only be observed with a heavy crop. If the crop is light the abundance of food materials manufactured obscures metaxenial differences. As competition increases metaxenial expression increases. Thus the method of comparing different males on the same spur will lead to exaggerated results and should be avoided.

Experiments

In my own experiments Fameuse apples differentially pollinated with Yellow Bellflower and McIntosh were used in the first trial. No striking differences were observed. It was found that the apples from the Yellow Bellflower cross showed greater variability of height and breadth and this difference was of a magnitude to be statistically significant. Yellow Bellflower, commercially speaking, was the better pollen, as the total number of fruits produced was larger and the apples appeared to average slightly larger and heavier. Since Bellflower pollen produced more seeds (5.8 against 4.6) per apple, the increased size could not be considered as a metaxenial effect. The increased variability in height and breadth of the apples from the Yellow Bellflower cross was not associated with increased variability in seed number and should accordingly be considered metaxenial.

The following year McIntosh apples were used with Red Astrachan and Yellow Bellflower as differential pollen parents. The average weight of apples varied as 91 to 79 gr. with a significance of 828:1 in terms of Fisher's odds. Seed number was statistically equal. The pH varied as 3.27 to 4.34 with a significance of the difference of 142:1. Acidity varied as 44 to 42 with a significance of 22:1. This result was considered encouraging and the experiment was repeated the following year. This time apples were harvested at four consecutive dates during development. In the apple the ratio of zygote to maternal tissue decreases during de-



HOW METAXENIA WORKS

Figure 6

We might crudely state the concept of metaxenia by asking: "Does the pollen of a red apple turn a normally yellow apple red?" Metaxenia in apples was first described by another name two centuries ago. Since that time many allegations of striking immediate effects of pollen have been reported in apples and other fruits. Many of the alleged influences of the pollen parent have not been confirmed by controlled experiments, but significant differences have been demonstrated to be due to the pollen used. In dates, the metaxenial effect on the time of ripening has great practical importance, and in apples metaxenial effects on keeping quality may have value in orchard practice.

velopment and this suggested that during the early growth stages of the apple metaxenial effects might be more pronounced than later. The four successive harvests were taken in mid-July, early August, mid-August, and mid-September respectively. On first sight it appeared that the experiment confirmed the theory. Red Astrachan produced the heavier crop at each harvest with the percentage difference in weight tapering off from 13 to 0 per cent from the first to the last day of harvest. Closer inspection showed, however, that seed numbers were also in favor of the Red Astrachan combination and that in all populations examined the correlation between apple size and seed number was positive and above 0.5. The actual results thus had to be corrected by the use of a regression factor. After this was applied two of the four harvesting dates still showed Red Astrachan to be responsible for the greater weight of the apples. The significance was 3:1 in one case and 4.6:1 in the other.

Due to the kindness of my colleague, Dr. Z. I. Kertesz, a large number of chemical tests was made from carefully graded samples of that year's crop (1932). They were analyzed in July, August, September, November and December. The McIntosh apples from the Red Astrachan p o l l e n consistently showed lower pH and higher acidity of the juice, the averages being 98.9 per cent with a significance of 6.3:1 and 109 per cent with a significance of 1341:1. A correlation between seed number and chemical composition did not exist within the range of this experiment. The apples also were carefully graded for size so that the influence of seed number was definitely eliminated. There was no indication that metaxenial effects became more pronounced or less distinctly expressed at successive dates of analysis. Thus the experiments of the two years using

Red Astrachan and Yellow Bellflower pollen on McIntosh apples show consistently that the average weight of apples from the Red Astrachan cross is greater, the pH lower and the acidity higher. These results represent metaxenial effects, expressed in the physiology of the apple.

The following year McIntosh was again used as female parent and was again pollinated with Red Astrachan and in addition with *Malus baccata* and *Malus atrosanguinea* both of which bear fruits not much larger than peas. The apples resulting from the *Malus baccata* and *Malus atrosanguinea* cross were distinctly inferior to those from the Red Astrachan cross, but this could be laid to a difference in seed numbers. From these three apple crosses successive chemical samples were taken of apples of comparable size, and determinations were made in August, September, October, November, 1933, and January, 1934. Acidity varied significantly each time, being relatively high in the Red Astrachan cross. The average of six experiments showed the Red Astrachan cross to be 8.6 per cent above the *baccata* combination with a significance of 26.4:1. *Malus atrosanguinea* as a male gave apples just as high in acidity as those from the Red Astrachan cross. *Malus baccata* in turn gave apples averaging 7.3 per cent lower in acidity than those from *M. atrosanguinea.* (significance 65:1). Total sugars read 3.8 per cent higher in the Red Astrachan cross than in the *M. baccata* cross (significance 78.5:1) with *M. atrosanguinea* intermediate, but not significantly different from either of the other crosses.

McIntosh apples produced by crossing with Red Astrachan, *baccata,* and *atrosanguinea* pollen differed from each other in phvsiological properties showing the following order of male parents for acidity: Red Astrachan and *atrosanguinea* > *baccata,* and for total sugars: Red Astrachan > *atrosanguinea* > *baccata.* A corresponding difference in keeping quality was observed in the three groups. Loss of weight was measured by weighing corresponding samples stored from the end of August until the end of December and until the end of January* respectively. In both weighings the Red Astrachan cross had lost 10 per cent less weight than the *Malus baccata* and *Malus atrosanguinea* crosses, with an average significance of 24:1.

Thus the results of this experiment corroborate the former and show that in the McIntosh apples obtained from the three different crosses there are significant differences in acidity and pH. Total sugars and keeping quality are also affected.

Keeping Quality

To return to intervarietal crosses two male varieties were selected which promised to give equal seed numbers. McIntosh was crossed with Wilson Red June and with Boiken. The two groups of apples produced were precisely alike in every respect except one. The apples were weighed individually in September and again in the following June. The average initial weight as well as the loss of weight in storage proved to be the same. Seed numbers agreed accurately in all samples. Chemical samples were taken from 10 relatively small and 10 relatively large apples of each group, the first averaging 67 and the latter 79 grams; these were analyzed for pH and acidity of the juice. Here again there were no detectable differences. The stored samples, however, did not have the same appearance after 9 months. The McIntosh × Wilson Red June cross showed only slight internal browning and practically no rotten spots. The corresponding group of McIntosh apples produced with Boiken pollen showed out of twenty apples which had originally appeared just as healthy as those from the Wilson Red

*This date was accidentally given as January 1 instead of January 21 in Table 6 p. 57 of Nebel and Kertesz (1934).

June cross, 5 apples completely rotten, 5 with large rotten spots and considerable internal browning in the remaining ones. This last feature again exceeded what could be observed in the Wilson Red June cross.

This better keeping quality of the Wilson Red June cross agrees with the expression of metaxenial effects of previous years and indicates that the sum of physiological effects may also be expressed in such a complicated phenomenon as "keeping quality."

In summary, 200 years of observations and measurements on metaxenia in apples are now available. If the uncritical experiments are sorted from the critical ones it appears that metaxenia exists as a distinct genetical phenomenon. In plants, however, nothing is known concerning the actual passage of substances from the zygote to the mother tissue. For this reason all experiments with plants merely infer that such passage may occur or that there is a reflection of the metabolism of the zygote upon the metabolism of the maternal tissue. In terms of the present work the chemical and physiological tests made in three years of experimentation showed statistically significant results each time.

It is concluded that metaxenia as a direct and specific influence of certain "factorial" characters transferred from the paternal genes in the zygote to the maternal tissue surrounding it could not be shown to occur and are believed not to occur. Metaxenia, however, exists inasmuch as two apples on the same tree with the same number of seeds and the same conditions of environment but originating from different kinds of pollen, may show slight physiological differences which may lead to small but consistent differences in acidity, size, keeping quality, general variability, pH and sugar content. The metaxenial expressions are listed in decreasing order of prominence as observed in the present experiments. This order may be changed and other characters may be observed as the work is carried to other combinations.

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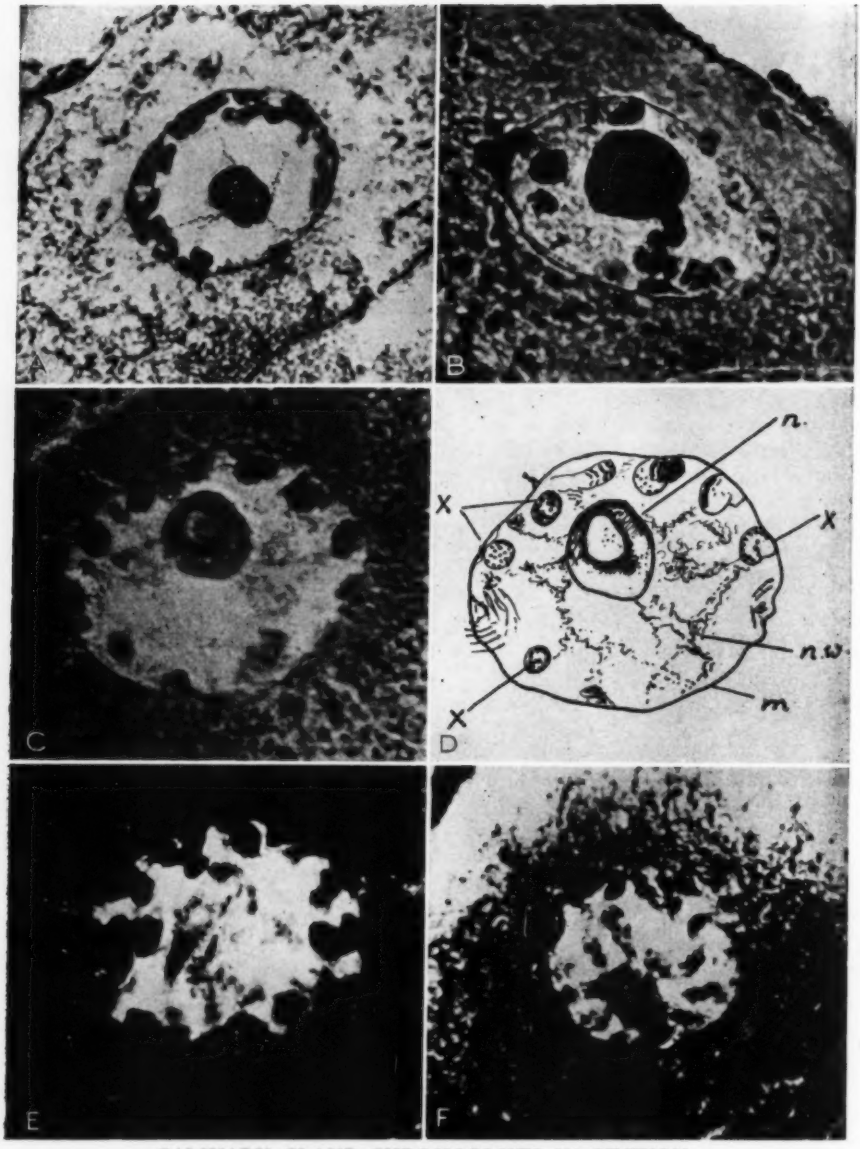

SALIVARY GLAND CHROMOSOMES IN SECTION

Figure 7

A detailed description of these photographs is given on the opposite page. The material is from three species of Drosophila (*A, B, E*), *D. subobscura;* (*C*), *D. immigrams;* and (*F*), *D. melanogaster*. *D* is a "sketch map" of *C*, showing the principal landmarks: *m*—nucleolus with vacuole; *nw*—nuclear net work; *x*—transversely cut chromosomes. Note that in the chromosome sections the chromonemata, which from an external view appear as strands, are distributed through the center of the chromosome as well as at the surface. These chromonemata represent, it is believed, the gene strings postulated by much genetic research, but visible in any detail only in such favorable material as the giant salivary gland chromosomes of the Diptera.

SECTIONS OF DROSOPHILA SALIVARY GLANDS

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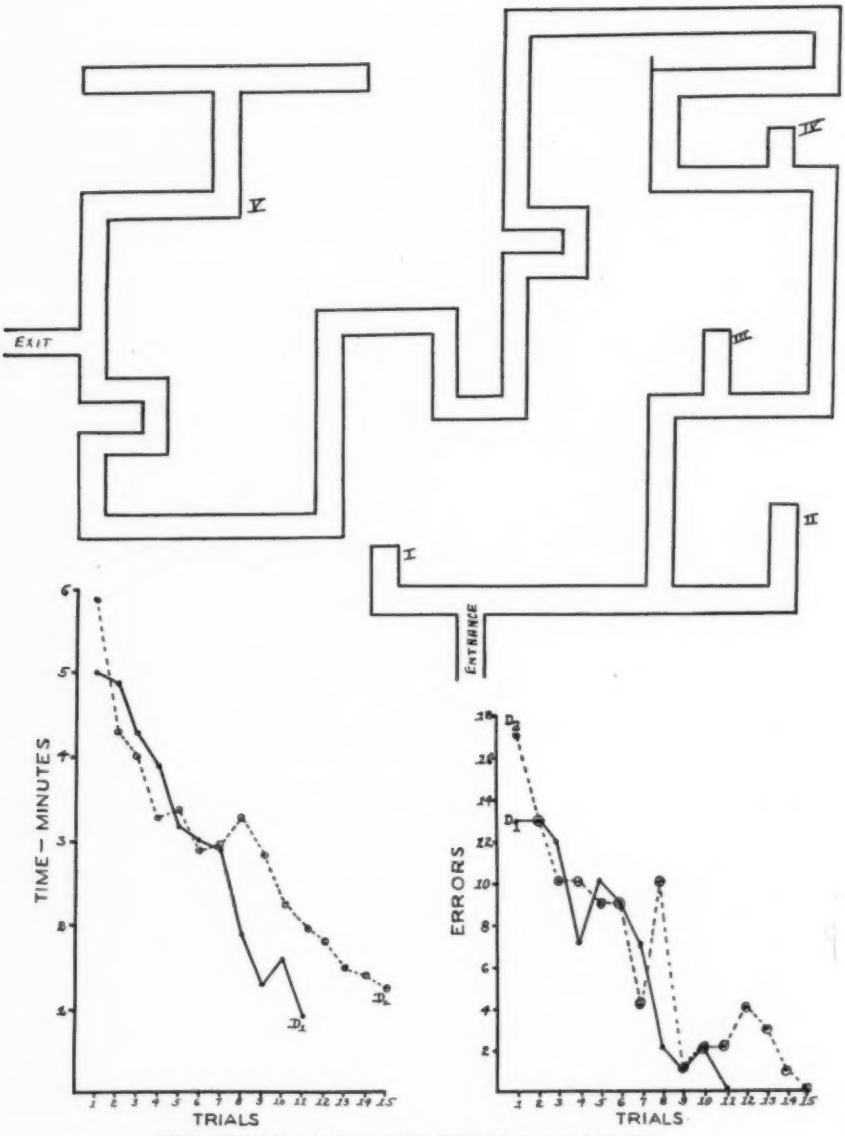
THE accompanying photographs are of sections of the salivary glands of several species of Drosophila, at a magnification of from 1,500 to 2,000 diameters, and are designed to show the organization of the nucleus. The sections were cut at 5 micra and stained either in gentian violet (Figure 7 *A-C*) or in iron haematoxylin (Figure 7 *D-E*). In the gentian violet preparations the nucleus is seen imbedded in the lighter staining cytoplasm, and the nuclear membrane, retouched in Figure *7B* only, is clearly visible. Iron haematoxylin stains the cytoplasm darkly, and so the outline of the nucleus is not so easy to make out in preparations stained by this method.

The diameter of the nucleus is around 25 micra, that of the nucleolus, seen in the center of the nucleus in Figure 7 *A-C*, about 7 micra, and of the chromosomes 2 to 3 micra. The diameter of the chromosomes appears considerably smaller than in aceto-carmine smears since there is some shrinkage and an absence of flattening.

Figure *7A* is from *Drosophila subobscura*, and shows the peripheral distribution of the chromosomes with the nucleolus in the center of the nucleus (it is not always centrally placed, but is always internal to the chromosomes), and several threads running from it to the chromosomes. These threads are part of a general network found in all species, but which in *D. subobscura* have a tendency to form radial connections between the nucleolus and the chromosomes. Figure *7C*, from *D. immigrans*, with Figure *7D* as an explanatory diagram, shows more of this network, but is of particular interest since the chromosomes are cut at right angles to their length, demonstrating that they are circular in section and that the chromonemata (gene strings) are distributed in their central regions as well as at the periphery. The nucleolus contains a vacuole, the light blob seen inside it. Figure *7B*, from *D. subobscura* again, shows the connection between one of the chromosomes and the nucleolus in this species, a connection not observed in the others examined. Figure *7E* is also from *D. subobscura* and is a section which does not include the nucleolus, but shows very well the general nuclear network referred to above. This network is believed to be those heteropycnotic parts of the sex chromosomes which are not included in the chromocenter. Figure *7F* is of a chromocenter in *D. melanogaster* which, like the chromosomes, is at the periphery of the nucleus, and sits over the nucleolus rather like a cap.

Some new and interesting facts about the relations of the nucleolus to the chromosomes and the chromocenter have been elucidated with the aid of these sections and will form the basis of a more detailed paper to be published shortly. The photographs were taken with the assistance of Mr. J. R. Thomas of the Dept. of Zoology, University College, London.



THE PENCIL MAZE AND THE TWINS' SCORES

Figure 8

Above is shown the outline of the pencil maze used in this experiment on identical twins. The maze is cut out of thin plywood. The subject is unable to see the maze and has to find his path through it by trial and error, sliding a pencil along the slot. Below are shown the time required to complete the maze and the number of errors made by the twins in fifteen trials. While there is some variation in the performance of the twins in individual trials, averages of groups of three consecutive trials are remarkably similar. This test is of possible value in twin investigations because it is little influenced by previous experience, and because the scores made can be compared objectively.

SIMILARITY OF IDENTICAL TWINS IN LEARNING A PENCIL MAZE

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A NUMBER of studies have been made with identical twins. These reports have repeatedly pointed out their close similarity in all kinds of mental traits. Unfortunately, many of the comparisons, until very recent years, have been made by ordinary observation, and are consequently less reliable than studies involving accurate measurements. The importance of the study of the similarity of twins in emotional traits is certain to receive increasing recognition in the future.

This study neither attempts to reveal similarities of mental traits nor likenesses in emotional traits, but aims (1) to show the similarity of patterns of identical twins in learning a pencil maze, (2) to compare the time required to complete each pattern, and (3) to reveal the similarity in the reduction of errors—entering blind alleys—in successive trials.

The use of a pencil maze has a number of advantages. In the first place, the learning of a maze is little influenced by the previous experience of the subjects, and thus it might be regarded as a novel situation. Secondly, while few accept the view that successful responses emerge through chance selection, great similarity of patterns of learning a maze may indicate that a great bulk of the children's motor responses is conditioned greatly by the identical structure of the twins. Thirdly, total patterns can be objectively compared.

The subjects in this experiment were identical twin girls, nine years of age and reared in the same home. Dorothy and Doris are so similar in anatomical features that the father assured the experimenter that even now he can not always distinguish instantly between them. Figure 9 shows their physical similarities. The experimenter observed that they put forth great effort to be different. They are, however, always dressed alike and it is only their immediate family who can distinguish Dorothy and Doris without extreme difficulty.

A report of their school teacher reveals considerable similarity in the quality of their work. The teacher rated Doris slightly higher in arithmetic and drawing while Dorothy was regarded as slighly superior in reading, spelling, and penmanship. The pencil maze, no doubt, challenged, to a degree, the mechanical ingenuity of the subjects. Thus a greater adaptation of Doris to the maze, as shown in the following data, might be due to her greater interest in activities involving some mechanical manipulation. In spite of the difference in their interests, their school marks are virtually identical; at the middle of the school year each girl had an average of 88 per cent.

A pencil maze sawed from 5-ply wood one-quarter of an inch thick; outside dimensions eight-and-one-half by eleven-and-one-half; runway one-quarter of an inch wide, was used. A wooden frame ten inches high was fastened to the four corners of the maze. This frame supported a black curtain on the top and around three sides, the rear side being left open for the experimenter to observe the subject's movements. An armhole with a sleeve furnished entrance through the curtain on the side of the subject. The maze was completely closed from the subject's view, permitting her to work with open eyes. Figure 8 shows the pattern of the maze. There are five blind alleys which are indicated on the drawing.

DORIS AND DOROTHY
Figure 9

Doris (D_1) and Dorothy (D_2) are so much alike even their father has difficulty in telling them apart. Their school marks are astonishingly similar, and their performance on the pencil maze is not markedly different.

Table I gives the number of errors made at each trial—blind alleys entered in the pencil maze—by the identical twins, Doris and Dorothy. The amount of time required to trace the entire pattern is also given. It will be noted that the number of errors and the time which was consumed during each trial are quite similar. Doris required eleven trials to produce a pattern without a single error. Dorothy attained the same achievement in fifteen trials. The greater interest displayed by Doris in the maze learning may account for this difference. When the errors for groups of three consecutive trials are averaged (presented in whole numbers), Doris made 13, 9, 3 and 1; Dorothy 13, 9, 5, 2, 1. The average number of minutes and seconds required to complete the maze, when groups of three consecutive trials are considered, are for Doris 4'42", 3'18", 1'57", 1'7" and for Dorothy 4'40", 3'7", 2'58", 1'58", and 1'20".

Figure 8 shows the learning curves of these identical twins in terms of the amount of time consumed in making a complete pattern at each trial; and also shows the number of errors made at each trial. As might be expected single trials do not begin to show the great similarity that is displayed when groups of successive patterns are considered. The above paragraph attempts to point out this similarity by the use of a composite of three consecutive trials.

Summary

1. In a novel situation, responses of identical twins seem to be unusually alike.
2. When the effect of environmental influences is removed the similarity in the responses of identical twins must be due to structure.
3. The number of errors — entering blind alleys — made by the identical twins are extraordinarily similar.
4. The time required for these twins to learn the maze shows considerable similarity of progress.

Table I. Total number of errors made at each trial--blind alleys entered in a pencil maze--by identical twins, Doris (D_1) and Dorothy (D_2); amount of time to trace and complete the pattern.

	No. of times subjects entered each blind alley										Total errors		Time for making complete tracing	
Blind alleys→	I		II		III		IV		V					
Trials	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2
1	0	5	2	3	5	0	6	5	0	2	13	17	5'0"	8'46"
2	0	2	0	2	6	1	4	4	3	4	13	13	4'50"	4'18"
3	1	2	2	0	4	2	4	4	1	2	12	10	4'13"	4'0"
4	1	0	0	0	0	2	5	2	1	0	7	10	3'48"	3'38"
5	1	1	0	0	2	3	4	1	2	4	10	9	3'10"	3'20"
6	0	1	1	1	3	2	3	2	3	3	9	9	3'0"	2'50"
7	1	1	0	0	2	2	0	4	1		7	4	2'50"	2'28"
8	0	2	0	1	1	4	0	3	1	0	3	10	2'45"	3'15"
9	0	0	0	0	0	0	1	1	0	0	1	1	1'18"	2'05"
10	0	1	0	0	1	0	0	1	1	0	2	2	1'30"	2'15"
11	0	0	0	0	0	1	0	0	0	1	0	2	0"	3'0"
12		0		0		1		1		2		4		1'40"
13		0		0		0		2		1		3		1'25"
14		0		0		0		1		0		1		1'20"
15		0		0		0		0		0		0		1'18"

A BABE IN THE GENETIC WOODS

Who Returns to Write a Book in Which Strange Genes Appear in Improbable Places

SCIENCE has remade much of the world we live in, and more science, in the sense of a wider and more sympathetic appreciation of the utility of a scientific attitude in solving the problems that confront us, seems to be a vital need at present. A recent ambitious attempt to bridge the gap between the lay world and the factual world of science leaves this reviewer with somewhat mingled feelings.* The author undoubtedly traveled far, listened much, and worked manfully to produce a volume of no little literary merit.

This popularized introduction to a number of "research fronts" of science in the middle 1930's has an added interest because it was the Scientific Book Club selection for November, 1935. The reviewer is fully aware of the difficulties with which such a committee must contend. With a program to maintain, some book must necessarily be chosen each month, and very likely the motives which impelled this selection were adequate at the moment. Nevertheless, some implications of a statement which bears the signature, but lacks the mental imprint, of the biologist members of a committee of five distinguished scientists†, does seem to have alarming implications.

When we come to "sell science" to the lay multitude we find ourselves immediately on the horns of a dilemma. The basic tools with which science works are simple, even though some of the gadgets which are used to isolate the factual raw material of science are complicated enough to suit even the ingenious Mr. Goldberg's cartooning. The tools of science are essentially an objective search for facts, and a gift for building up these facts into a conceptual structure that gives an harmonious and accurate picture of the Universe in which we live. This technique is diametrically opposed to many processes which are today accepted as valid guides to ordering our lives as human beings in 1936 society. Here verbalization, emotionalism, wish fulfillment, and a host of other "isms," cults, and magic formulae are accepted in the best circles as sound bases of enlightened social behavior. If science has any message for humanity at this period of social travail it is of the need for abandoning the appeal to magic and substituting for it the appeal to fact. Unfortunately the other horn of our dilemma protrudes at this point. In a "fairy-story" society "mere facts are so drab and dull." Therefore we must sugar-coat them with a "story." We must cast our researchers in the fiction mould, with microbe, or gene, or electron as the villian of the piece, and with Consecrated Nemo of the Laboratories as the hero. In the sugar-candy process the facts get the worst of it, and our public gets nowhere in finding out what science is all about, and may well conclude that it is just one more sideshow trick.

Scientists speak a specialized jargon, and are likely to be intensely obsessed with the particular corner of the unknown in which they are adrift. Thus few scientists are in position to act as interpreters to the general public, or even to specialists in other fields of scientific endeavor. Literary dissertations on scientific subjects range all the way from serious and sincere attempts

* JAFFE, BERNARD. Outposts of Science. Pp. 547. Price, $3.75. New York: Simon and Schuster, 1935.

† The Committee which makes these awards is as follows: Edwin G. Conklin, Kirtley F. Mather, Arthur A. Compton, Harlan T. Stetson, and Edward L. Thorndike.

to interpret research discoveries concerning nature and man, to maunderings that make the laboratory workers of today a sort of glorified Voodoo cult. This latter school of "scientific enlightenment" undoubtedly has the greater box-office appeal, because people are interested in magic and "understand" quite readily what it is all about. The question at this point is: how far can we go in attaining the desirable end of engendering intellectual honesty (even to the extent of using it as a condiment to flavor our consideration of human affairs) by the oblique approach of the circus barker and the medicine man?

The matter is thus crudely put because some statements made in connection with the book in question are an excellent demonstration of the working out of this philosophy. On the inside of the jacket in which the book is distributed is a statement signed by the Committee of Award, which reads in part (with the crucial sentence italicised by the reviewer) as follows:

> * * * Those who read *Crucibles*, by Bernard Jaffe, a book which won the Francis Bacon award for humanizing knowledge, will not need to be told that *Outposts of Science* captivates the imagination from cover to cover. Mr. Jaffe has a way of telling his story with vigor and with an enthusiasm that is contagious. *The very fact that the author surveys so many various aspects of scientific work, in which no one man can hope to be proficient, gives assurance that the book is for the general reader.* One does not become bewildered with the technical details of the specialist.
>
> The book, however, carries the air of authority. To become accurately informed, the author traveled far and wide to interview noted heroes of science. * * *

The difficulty lies in deciding when a *lack of proficiency,* which appears to be advanced as a *sine qua non* of successful scientific authorship, ceases to be a virtue, and becomes a stumbling-block. How much "lack of proficiency" can we have before we cease to be interpreters of science and degenerate into the voodoo class of purveyors of modern magic? If the chief message of science is to stress the need for an objective consideration of facts, can we carry it to lay Garcias by failing egregiously to know what we are talking about? This question of the popularization of science is a tremendously difficult and important matter. The reviewer takes emphatic exception to the view that this desirable end can be effectively furthered by what seems to be an endorsement by scientists of ignorance as a requisite of successful interpretation. He proposes to demonstrate the kind of pitfalls this leads to by considering how Jaffe's "lack of proficiency" in genetics has guided him in interpreting that science in its bearing on research into the causes of cancer.

In doing this the reviewer is frankly going to turn his back on some of the excellencies of the book, because he feels that a principle of no little importance is involved, whose implications require the space available for an adequate demonstration. Any intelligent person can by reasonably diligent application explain the gene theory, linkage, crossing over, etc., in very intelligible terms, as Jaffee has done. Reference to this chapter may very well have led the biologist members of the Committee to overlook the astonishing genetics contained elsewhere in the same volume, and to concur in giving the book a "passing mark." The test of the lack of proficiency philosophy comes when we attempt to interpret knowledge in its broader aspects and implications. Here it seems that Jaffe's genetics have sadly gone back on him. The pity is that recognized leaders in American science seem to join in the applause. Such an endorsement may have rather far-reaching effects. Thus the magazine, *Time,* usually accurate, penetrating, and caustic in comment, repeats, in discussing Miss Slye's work, in its issue of August 31, some of the genetic inanities of which Jaffe is guilty. Possibly the endorsement of five scientists influenced the editors of *Time* to accept questionable statements without comment. Certainly the rebuttal of such inaccuracies is complicated by so great a weight of authority.

In the chapter on cancer the urge to write convincingly about a subject with which he is not proficient lays Jaffe open

to the criticism of producing a biased and befuddled discussion. The tragedy is that the layman is not in position to realize that he is being fed, along with a considerable diet of facts, a goodly dressing of "hooey." The author's interview method of treatment undoubtedly partly accounts for this. It produces a readable and sometimes exciting result, but it fails to give a well rounded picture of the cancer problem as it is understood today. This fact would be small ground for criticism were it not that definite claims are made that this is exactly what the reader is getting. Thus the chapter title reads as follows:

CANCER

Man Struggles with the Anarchy of the Cell

With Special Attention to the Epochal Work of Maud Slye

If the chapter had been headed in the sense of the second subtitle, with the possible addition of "With Readings from Her Poems," the reviewer would have no valid complaint. Since the chapter does not deal broadly with the cancer problem as a whole, but primarily with Maud Slye's contribution to the subject, the implication given by the chapter heading and in the Committee's blurb,* that the cancer problem of 1935 is adequately discussed, is wholly misleading. The result is unfortunate for several reasons. In the first place it gives the laymen a distorted idea of the present state of our knowledge regarding cancer. Furthermore the discussion will inevitably arouse feelings of irritation and resentment in the breasts of many other workers who have done very important work in this field, and whose contributions are ignored.

One gets the impression after reading this chapter that Maud Slye (whose contribution the reviewer is not attempting to evaluate) has opened up practically all the avenues of attack on this problem. This implication is by no means correct. Jaffe as an individual equipped with even an average lack of proficiency may well be pardoned for having failed to do an adequate job of evaluation. Should a committee of scientists, even though it recommends the book, subscribe to statements of very questionable accuracy regarding a matter of very considerable importance?

This attitude is evident in an early paragraph of this chapter: "Today there is some light coming from at least one spot on the wide front of the cancer battle line. It is the light kindled by a woman who 25 wears ago consecrated her life to the solution of the cancer problems * * *." The implication is strong, and it carries through the chapter, that this one light is about the only one that has been shed on this problem in recent years. Granting the importance of this contribution, what of many other workers who have also given many years of their lives to this basic problem of cancer genetics, and whose contributions are fully as important? Only three other American workers active in research on the genetics of cancer are mentioned by name, and their work is referred to only as proving earlier work by Miss Slye. Is anything further needed to demonstrate the one-sided nature of this discussion?

Jaffe further intimates that by a criticism of Miss Slye's work published by another geneticist her chances for the Nobel prize were lessened. It would seem to be obvious that if a scientist's work is worthy of that honor, it can withstand criticism directed at it by contemporary workers. It is a mistake to attempt to exert pressure for any candidate for the Nobel prize. This award has been singularly free from such undesirable influence. It should remain so.

Is Cancer Susceptibility a Recessive?

Many statements are made by Jaffe regarding the genetics of cancer which would hardly be conceded to be correct

*"In Chapter 4, the reader will find the very latest account of the war against cancer, that subtle and mysterious multiplication of cells not yet under control. * * *"

by many recognized authorities. A motif that permeates the entire chapter as an "overtone" of the above preoccupation is the concept that susceptibility to cancer is inherited as a simple mendelian characteristic:

> First, nonsusceptibility to mouse cancer acts as a Mendelian *dominant;* susceptibility to tumorous growths as a *recessive character.* The presence of one gene seems to mean the difference between cancer-susceptibility and nonsusceptibility. Or as Miss Slye has worded it in her last report of 1933, "Cancer involves a complexity which differs in only one gene from the complexity involved in insusceptibility." At this late date, few would dare quarrel with this statement, although some, like Loeb, the pioneer in cancer heredity, hold to a difference in several genes. * * * This great contribution by Maud Slye can no longer be denied by fair-minded men.

As a matter of fact, many "fair-minded men" cannot overlook a mass of facts coming from other laboratories that do not substantiate this claim. Readers of the JOURNAL will recall Dr. L. C. Strong's recent contributions to this subject in the JOURNAL. Dr. Strong has many years of research in cancer genetics to his credit, and his contribution goes entirely unnoted in the work in question. It will be recalled that Strong records the production of two highly inbred strains, one of which showed a higher susceptibility to cancer than the other. It is obvious to any "fair-minded man" that these differences are not due to a simple mendelian difference in this strain, and it is not in many other strains that have been studied. It is not necessary to raise hundreds of thousands of mice as has been done in Miss Syle's laboratory to establish the inheritance of a simple mendelian characteristic. The job can be conclusively done in as little as a half dozen generations. The very fact of the continuation of this research over twenty-five years speaks volumes in proving that there is more to the cancer problem than can be explained by a simple 3:1 mendelian ratio plus a dash of carcenogenic tar. This difficulty is hinted at in the next paragraph:

> The second clear fact which has emerged from her work is that in addition to this internal factor of inheritance, the external factor of irritation must be present to produce cancer, in most cases. "The inheritance of cancer susceptibility alone is probably not always sufficient to insure the occurrence of malignancy," says Miss Slye. "An external factor acting with internal factors upon a susceptible soil is probably the cause of cancer." Chronic irritation in a mouse of a pure noncancerous parentage will produce no cancer. Chronic irritation of a mouse susceptible to cancer according to its known pedigree will produce cancer. A mouse free from irritation, even though it comes of a cancerous background, has in many cases not developed a neoplasm. "In a family of mice with a high frequency of cancer of the skin it is possible to prevent the occurrence of cancer by preventing chronic skin inflammation. This has been done in my laboratory. In a family with a high incidence of cancer at the base of crooked and overgrown teeth, it is possible to prevent such cancers by keeping the teeth cut short and thus preventing overgrown crooked teeth with consequent pressure on the soft tissues."

These questions of the number of genes involved in cancer inheritance, and of the secondary agents which may act as "triggers" to initiate tumor growth are tremenodusly important. The problem is by no means as simple as this statement would lead us to believe. In this connection reference might well have been made to the very important work reported by Little and others a few years ago,* in which a maternal inheritance of a tendency to breast cancer was reported. Since that preliminary report, increasing evidence has been produced by workers in the Jackson Memorial Laboratory that there is in mice a definite inheritance in the maternal line of a predisposition toward cancer of the breast. This fact has great potentialities of practical application and implication in man, and from the point of view of cancer prevention it is significant that in human beings a higher percentage of cancer occurs also in females than in males. Mouse genetics, plus human cancer statistics, suggest the possibility of a maternal inheritance in the human species. These facts may legitimately be the starting point for research in human genetics. Such an approach is quite in contrast to the bold and very questionable leap from mice to men noted below. The

*_Science_, Vol. 78, Page 465; 1935. _Science_, Vol. 82, Page 228; 1935.

complete failure to mention this very significant and important recent contribution is only a sample of many similar failures throughout the chapter. If the chapter had adequately presented "man's struggle with the anarchy of the cell," mention of such facts could not have been utterly ignored.

The implication that an irritant is almost universally necessary to produce a cancer is abundantly not borne out by the facts from other laboratories. Strong, Little, and others report strains of mice in which cancer occurs regularly without any external stimulus. In other strains an irritant stimulus will produce a cancer. Furthermore, an irritant stimulus that will consistently produce cancers in some strains will not produce them in others. Here again much more knowledge is needed.

Mice and Men

The very naive nature of this genetic discussion is indicated by the following:

> Mice and men. Miss Slye has been interested in cancers of both. Her work has centered around the problem of cancer prevention rather than of the cure. In mice, she has actually succeeded in eliminating cancers by persistently mating through successive generations pure noncancer strains with hybrid susceptible cancer carriers. After several generations she obtained cancer-free progeny. Somewhere in that elaborate crossbreeding process, the cancer factor had been wiped out. She had worked similar miracles before. By such controlled breeding, she had got rid of albinism and the dancing habit of Japanese waltzing mice. "If I wish to produce any kind of mouse," says Miss Slye, "I can do it. I can make him to order. I have produced cancer in mice and then bred it out."

Even an elementary acquaintance with genetics would put the reader on his guard that the author was bordering perilously on the ridiculous. If, as is stated earlier, cancer is a simple mendelian recessive, the statement "Somewhere in that elaborate crossbreeding process, the cancer factor had been wiped out," is a priceless example of the kind of inane statements to which a lack of proficiency leads us. Any geneticist knows that in order to "wipe out" a recessive factor in a given stock it is necessary to make certain definite test matings of normals with recessives to discover the heterozygous "carriers" of recessive genes. By eliminating these carriers (which is not easy when small progenies are involved) it is possible to produce in a few generations a stock entirely free from the recessive in question. There is no magic in an "elaborate crossbreeding process." To do the trick in many generations by such a means may be a miracle, unless we credit it to the luck which is proverbially alleged to be on the side of fools and infants. Here it seems that the facts are fully as interesting as the implication of the occult which Jaffe invokes.

Jaffe puts his heroine on a very tough genetic spot with the concluding quotation. Any geneticist can "make any kind of mouse to order" where such well-known genes as albinism and waltzing are concerned, and "recessive susceptibility" should add nothing to the complexity. In informal conversation with the laity such a statement by a specialist would be eminently permissible, but embalmed in the embarrassing rigidity of paper and ink these seventy years after Father Mendel raised peas, the effct is far less pleasing. A fair analogy would be for a chemist to expect his colleagues to rush the medals because he burned hydrogen and got water, a stand which could result only in getting him into an abundance of that useful compound warmed to near the boiling point.

In man the difficulty of arranging the necessary test-mating makes the elimination of recessive genes extremely difficult, if not practically impossible. On the other hand a dominant gene, in which all of the individuals carrying the gene show the character, offers no theoretical difficulties whatever. In a single generation a dominant gene that is clear cut in its expression can be entirely removed from a population by withholding from reproduction all individuals manifesting the character. (The feasibility of this in the human species is another matter.) In such a case, the theoretical and practical difficulties are reduced to a minimum. This

is very much in contrast to the situation with recessives, in spite of which witness the following:

> Men cannot be locked in cages and mated like mice or guinea pigs. Since our knowledge of human genetics is so limited, Maud Slye has been obliged to jump from the conclusions of her mice experiments to implications regarding cancer in men. At the Mohonk conference which met in 1926 to consider the problems of cancer, Miss Slye, who was invited to attend though not to read a paper, took occasion to introduce her program. No cure being known, she announced her belief in the control and prevention of human cancer upon the basis of the knowledge she had built up in the genetics of mouse cancer. Men frowned and even attacked her. Dr. Charles J. Hastings of Toronto insisted that "the public must be assured that cancer is not hereditary."
>
> Maud Slye felt that this opposition was unwarranted. Her picture, after all, was not so dismal. She had emphasized time and time again that susceptibility to cancer was not a dominant character, but a recessive. "This," she said, "is most encouraging, for it means that large numbers of individuals are by inheritance exempt from the probability of cancer."

This statement seems also to be genetic gibberish. Obviously the mere fact of dominance or recessiveness tells us nothing about the probability that a given individual in a given population will exhibit a given trait. Thus, the blue eye of the Nordic tends, by and large, to be recessive to the more heavily pigmented iris colors. Komai has recently pointed out that this blue-eye allelomorph appears to be entirely lacking in the Japanese race. Thus 100 per cent of the population of many parts of the Scandinavian Peninsula would by inheritance be "doomed" to exhibit a recessive trait that 100 per cent of the inhabitants of the Japanese Archipelago would "by inheritance be exempt from." As a usual thing human populations do not show so complete a unanimity in regard to a given pair of allelomorphs. The only way in which we can hazard predictions regarding the frequency of appearance of a given dominant and recessive pair is by a hasty counting of noses with respect to their frequency of appearance in a given population. The fact that in the United States cancer is in second place as a cause of death after 40 demonstrates that Miss Slye's postulated recessive gene must be so very widely disseminated that the chance of being able to eliminate it without eliminating 75 per cent of the human race is so slight as to be practically nil. To imply that the fact of its recessiveness is a cause for loud Hosannas is under the circumstances calculated to leave the geneticist considerably astonished.

From this we must conclude: (1) that if Jaffe has correctly quoted Miss Slye both of them should borrow a few up-to-date books on elementary genetics and read them carefully before leaping with such abandon from mice to men, and (2) in any event Jaffe should have done this before he undertook to tell the world about genetics and cancer. In the light of such statements the wisdom of the Nobel Prize Committee (as discussed above) seems to be abundantly confirmed.

Progress in the solution of the cancer problem demands a coordinated research attack on a wide front. The reviewer is not in touch with the situation on much of the "cancer front," but he can say that research in cancer genetics would progress faster in many laboratories if more funds were available. An enlightened public interest in this problem would undoubtedly hasten the day when we may be able to struggle intelligently with the growth anarchy which is cancer. From this book the reading public would get a caricature of the actual state of the "cancer outposts" as a whole in 1935. Adequately told, the story is indeed fascinating, and one which should interest as many people as this half-told-tale. Possibly public demand might be built up for more fundamental research which is so badly needed.

One tragedy of the "lack of proficiency" school of scientific enlightenment is that one sometimes comes back with a load of fool's gold, when all about are tons of the real ore.

ROBERT COOK

AN INTRODUCTION TO EUGENICS*

THIS is a book containing 173 pages of text, some of them partly or largely occupied with one or more of the 41 figures which are presented. There are 11 plates and the book carries two appendixes, one of which is bibliographical, and a glossary of 13 pages. The author has courageously confronted herself with the job of condensing the material from 156 bibliographical items and presenting it, in approximately that many pages of text, in a way that would be intelligible to students previously unacquainted with the subtleties of genetic theory and practice.

The advance on this magnificent objective had to be rather too rapid for thoroughness, and the reviewer, in his ungracious task of mopping up the conquered terrain, naturally found a few solecisms, alive and very revengeful, and some evidence that, in the hurly-burly of attack, some violence had been done to the rules of organized biology.

The book first outlines the early history of Eugenics, with Galton thoughtfully occupied at his desk, and then takes up the subjects of cell structure, mitosis, gametogenesis and early embryological development. In describing the heterotypic division in females the author makes the statement, "They" (the chromosomes) "merely separate into a maternal and a paternal group, and one group goes to one end of the spindle and the other group to the opposite end." This is followed, in speaking of spermatogenesis, by the statement: "The chromosomes pair into the maternal and paternal groups and become reduced in number." Students would have some difficulty in reconciling these descriptions of chromosomal movements with the data upon Mendelian segregation that immediately follow.

Chapters 4 to 9 inclusive deal with human inheritance in mental and physical abilities, including disease resistance and blood group inheritance. The evidence of heredity is largely presented in the form of pedigree charts, the significance of which is beyond the ability of inexperienced students unless each of the charts were accompanied by much more explanatory material than the author included. It seems probable that the statement: "According to a survey of the Mental Deficiency Committee in the urban districts of Great Britain idiots make up 3.6 per cent of the population, imbeciles 16.6 per cent and the feeble-minded 80.3 per cent." will be tagged by English readers as a bit thick. Most anthropologists, too, would probably fail to concur in the statement that: "It is highly probable that the white race is an albinic variation which has arisen through loss of pigmentation."

In the table of blood groups, group I (O) is called the universal recipient in spite of the attending statement that group I serum will agglutinate all incoming cells, while group IV is called the universal donor with the accompanying statement that group IV (AB) cells will be agglutinated by the serums of the three other groups. It is suggested too, that racial differences in blood groups "may depend partly on food habits, since group II, preponderant with the flesh-eating English, is very low with the vegetarian Hindus," an inference difficult to reconcile with a strictly hereditary basis for blood group differences.

A rather brief chapter upon twinning does not include the very important data upon identical twins reared apart. In fact the rather questionable statement "Nor is it known that identical twins change in different environments" is unfortunately situated opposite the comely features of Mary and Mabel who armed Newman with his largest mental test difference that might be causally connected with an environmental difference.

*Brown, Mary J. Pp. 217. Price, $3.00. Boston: Chapman and Grimes, 1935.

The paginal arrangement of material is rather good, the glossary is accurate and the index fairly comprehensive. The author does not have the habit, by no means rare even among the "big shot" authors of elementary texts, of making statements in so guarded a fashion that they cannot be nailed as errors and yet admit of so many interpretations that they lead inevitably to mistakes in inference and to a healthy exasperation among students. The reviewer thus feels a little unsportsmanlike in calling attention to such honest errors as have been mentioned, and does not feel that the uncovering of any more of them would serve a useful purpose. To be very useful as an introduction to eugenics, the errors in fundamental genetics should be corrected and the book should either be narrowed in scope or enlarged in explanatory material, so the included subjects could be adequately introduced to a reader lacking previous preparation in the field.

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HANDEDNESS: RIGHT AND LEFT*

THE special difficulties involved in the genetic analysis of handedness are well known: the refractory nature of human material, and the lack of a decisive test for congenital hand preference. Recent work by Peterson (*Comp. Psychol. Monographs*, vol. 9, 1934) indicates that even laboratory animals present similar difficulties, for, in the case of the rat, at least, "handedness" appears to differ according to the criterion used.

Dr. Wile's book is not primarily concerned with the genetic aspects of handedness, although there is a fair amount of material of genetic interest scattered through the book and some space is given to a summary review of such genetic studies as have been made, without, however, including pedigrees or data. The author has overlooked the rather extensive material of Chamberlain presented in this Journal (vol. 19, 1928) which, incidentally, is consistent with the hypothesis that left-handedness is a mendelian recessive whose expression is complicated by "somatic overlapping" with normal (i.e., with right-handedness, due to imitation, training, etc.) in about 50 per cent of the homozygotes.

The author's viewpoint is primarily anthropological rather than biological. Although much information is presented regarding asymmetry throughout the plant and animal kingdoms, the greater portion of the book is devoted to such subjects as hand preference in primitive man (concerning which there is considerable, though conflicting, evidence, from the mode of construction of implements and the manner in which the cutting edges are worn), the luck idea and hand preference, and hand values in magic.

A chapter on the causation of dominant handedness reviews the numerous hypotheses which have been proposed, with special attention to speculation regarding the possible influence of the earth's rotation on the origin of hand preference. This idea is apparently original with the author, but the reasoning in support of it is unfortunately somewhat difficult to follow.

One cannot glance through Dr. Wile's "Handedness" without being impressed by the amazing array of out-of-the-way material which it contains, and it is a volume which the general reader as well as the specialist interested in problems of handedness will doubtless find entertaining as well as instructive.

The bibliography is extensive, although omissions are not difficult to find, such as the paper of Chamberlain cited above, and the very important memoir of Woo (*Biometrika 20A*, 1928).

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*HANDEDNESS: RIGHT AND LEFT, by Ira S. Wile, M.S., M.D. Pp. xiii + 439. Index and bibliography. Boston: Lothrop, Lee and Shepard Company, 1934.

ENDOCRINE WEIGHTS OF THE BANTAM FOWL

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RECENT investigations of the relationship of the endocrine glands to growth have induced us to make a study of these organs in the bantam fowl. No data on the endocrine weights of the bantam fowl were found in the literature available and only a limited number of pertinent references were found concerning the endocrine weights in the standard breeds of fowl. This paper will present some observations and measurements of the endocrine glands of English game bantams. Fourteen adult males and fourteen adult females raised from a single cock and two hens comprised the group from which this preliminary study was made.

The birds, which were hatched in the spring of 1934, were allowed free range on a nearby farm and were fed standard grains and mash feeds. The birds were brought into the laboratory in small groups for autopsy. They were starved for 24 hours, weighed alive and then killed with illuminating gas. All glands were dissected out carefully, trimmed of fat and connective tissue under the microscope, and weighed in a small chambered vial to the nearest tenth of a milligram on an analytical balance. Weights were made of the hypophysis, thyroids, parathyroids, adrenals, spleen and testes. The results are found in Table I.

The birds were all sexually mature when autopsied, although the males were less than a year old; the females were sexually active or had laid eggs. The average age of the males, when killed, was less than the average age of the females. However, the endocrine weights and the body weight of a male three years old were within the limits of variation of the weights of the cockerels. The birds were autopsied at times which extended over the reproductive period, in an attempt to rule out any change which might occur with the varying sex cycle. Cruickshank[2] showed that the thyroids of female birds became smaller during the period of egg production.

The actual endocrine weights (Table I) are all smaller than those of a normal breed, i.e., white leghorns. When the weights are calculated on the basis of a per cent of body weight and are compared with similar results for the other breed, there is a decided difference noted (Table II). The endocrine weights of normal breeds were taken from the work of Juhn and Mitchell[3] on brown leghorns, from Latimer[6] on white leghorns, and from Landauer and Aberle[5] on white leghorns.

According to the standard of perfection for the domestic fowl, the brown and white leghorns are similar in respect to body weight although the body weights of the brown leghorns used by Juhn and Mitchell were considerably lighter than those of the white leghorns. There was a marked difference in the endocrine weights, based on a per cent of body weight, between the white leghorns and brown leghorns, which was due to the lower body weight of the latter. The weights of the endocrine glands, with the exception of that of the hypophysis, based on a per cent of body weight, were fairly similar in the two groups of white

*Aided by grants from the Rockefeller Foundation.

leghorns. Unfortunately, Latimer did not give the endocrine weights according to sex but only the average was presented. Data on birds approximately 280 days old were chosen from Latimer's tables for comparison and the birds used in Landauer and Aberle's work were 240 days old.

Hypophysis

It is interesting to note that the hypophysis is definitely larger in the bantam than in the white leghorn when it is compared on the basis of 100 grams of body weight (Table II). In the female bantam, the hypophysis weighs .748 mgm. per cent; in the male, the hypophysis weighs .765 mgm. per cent. Latimer found the hypophysis of the white leghorn to weigh .6 mgm. per cent over a wide range of body weights and age (from 1400 grams to 2600 grams body weight and up to 3 years of age). Landauer and Aberle found the hypophysis to weigh .383 mgm. per cent(female) and .431 mgm. per cent (male) and Juhn and Mitchell obtained hypophyseal weights twice those of the bantams. The abnormally low body weights of the brown leghorns distort the calculated results of the endocrine glands and for this reason, it seems desirable to emphasize further comparisons between the bantam fowl and the white leghorn.

There is no indication of a sex difference in the weight of the hypophysis of the bantam fowl when compared on the basis of 100 grams body weight.

Thyroid

The weight of the thyroid of the bantams, calculated as a per cent of body weight, is distinctly lower than that of the leghorns. From the results in Table II, it is seen that the thyroid weights of the leghorns examined by Landauer, which are the smallest for the normal breeds, are approximately twice the weight of the thyroids of the bantams. The thyroids of the male birds in all breeds studied are slightly heavier than the thyroids of the females, on the basis of equal body weight. However, there is not a significant sex difference in the weights of the thyroids in the bantams.

Adrenals

In contrast to the hypophyseal and thyroid weights, the relative weights of the adrenal glands are remarkably similar in all groups with the exception of the brown leghorns. This latter discrepancy can be explained by the low body weights already mentioned. There does not seem to be any sex difference in the size of the adrenals when compared as above.

Other Glands

Unfortunately, a satisfactory comparison between the other organs weighed and those of the normal breed cannot be made because of the lack of data on the normal breeds. The relative parathyroid weight in the bantam is similar to that of the male brown leghorn. There is no sex difference noted in the size of the parathyroids in the bantam fowl. The spleen weights of the bantams and the white leghorns are also quite similar (Latimer's data in Table II). There is no sex difference in the weight of the spleen in the bantam. The thymus glands of the bantams vary greatly in weight and no sex difference is noted. Latimer found the thymus glands of 280 day old birds to weigh .05 grams per cent which is definitely smaller than the thymus weights of the bantam (.0946 grams to .1081 grams per cent). The ovaries were not weighed because of extreme variation. The average weight of the testes of the bantams is .605 grams per cent and that of the white leghorn (Landauer) is .363 grams per cent.

Discussion

The results of these observations indicate that in the bantam, the thyroid gland is considerably lighter and the hypophysis is slightly heavier, in proportion to body weight, than in the larger standard breeds. It is interesting to note that the endocrine glands which function primarily in growth,

are the ones which show weight differences. The adrenals, which ordinarily are not considered to influence body size in a manner comparable to the hypophysis and thyroid, are approximately the same size in both types of birds when compared on a weight basis. Although the number of animals used is small, the uniformity of the weights of the glands, particularly in the female, seems to make these results significant. Insufficient data from normal birds on the weights of the remaining organs, precludes further discussion of their comparison.

There are certain types of inherited dwarfism, such as occur in mice, which have been correlated with hypophyseal deficiencies (Smith and MacDowell[9]), and these deficiencies have been corrected by hypophyseal treatment. These investigators showed that in female dwarf mice, the weights of the hypophysis calculated on a percent of body weight are .003 to .005 grams as compared to .007 to .008 grams for normal mice. The thyroids of the dwarfs were so small that dissection and weighing was impossible. It is possible that the thyroids were also smaller in proportion to body weight in the dwarf mice than in the normal mice.

A type of dwarfism has been re-

Table I. Endocrine Weights of Bantam Fowl

	Age (days)	Body weight (grams)	Hypophysis (mgms.)	Thyroids (mgms.)	Parathyroids (mgms.)	Adrenals (mgms.)	Thymus (grams)	Spleen (grams)	Testes (grams)
					(Male)				
	159	945	6.4	42.0	7.8	86.0	.8124	1.1314	4.8618
	191	769	4.5	53.8	9.3	79.6	1.0972	1.2972	1.1772
	192	852	5.8	50.0	6.0	63.8	.9268	.9668	2.7138
	211	956	6.7	43.9	5.8	82.5	1.1557	1.2357	3.9494
	241	958	6.2	42.0	14.4	100.0	.7780	2.0910	8.0070
	242	804	6.8	27.6	5.6	84.0	.3926	1.0060	4.4360
	242	687	6.6	39.2	6.0	56.2	1.3626	1.2102	3.6697
	243	636	7.8	40.6	20.7	81.2	.6222	1.1472	3.8462
	243	838	4.5	46.5	19.9	66.5	1.0165	.8045	4.9165
	303	952	8.4	65.6	9.0	80.0	.3164	1.1700	5.5140
	304	779	8.0	40.6	9.8	68.0	.2800	.9486	8.4890
	311	806	5.6	80.4	5.6	59.2	.4854	1.0494	5.8410
	311	726	4.6	56.2	10.8	e0.2	.6250	.6760	5.8500
	311	635	4.4	61.2	8.8	66.8	.8806	.7900	5.3940
Av.	250	810	6.2	49.3	10.0	73.9	.7665	1.1086	4.9039
					(Female)				
	175	695	3.7	33.4	9.4	54.4	.4838	1.1414	
	178	642	4.0	22.2	5.1	62.6	.4846	.7726	
	179	626	4.2	24.3	5.8	52.8	1.0320	1.2820	
	392	564	5.3	48.1	4.8	57.2	.5886	.5751	
	392	560	4.4	37.2	6.8	53.8	1.0028	.6738	
	392	505	4.0	24.4	9.4	53.8	.3558	.4744	
	394	846	5.0	43.0	7.2	65.1	.1386	.6722	
	411	631	4.7	38.5	9.4	57.4	.6272	.8064	
	411	526	4.6	26.2	14.8	67.2	.3687	.5218	
	411	545	5.1	33.4	3.8	43.8	.2317	.8634	
	430	573	4.0	28.4	6.0	51.2	.2028	.6908	
	435	579	4.7	31.3	7.8	51.5	1.4960	.6475	
	436	452	4.0	45.6	9.3	47.1	1.4616	1.0520	
	443	493	3.8	24.7	6.3	43.7	.4263	.5473	
Av.	363	588	4.4	33.1	7.6	54.0	.6357	.7657	

Table II. Comparison of Endocrine Weights of Bantam and Normal Fowl as a Percent of Body Weight

	Hypophysis (mgms.)	Thyroids (mgms.)	Adrenals (mgms.)	Parathyroids (mgms.)	Thymus (grams)	Spleen (grams)	Testes (grams)
Bantam ♂	.765	6.08	9.12	1.23	.0946	.1368	.605
Bantam ♀	.748	5.63	9.18	1.28	.1081	.1302	-
White leghorn ♂ (Landauer)	.431	11.71	9.83	-	-	-	.362
White leghorn ♀ (Landauer)	.383	10.21	8.52	-	-	-	-
White leghorn ♂+♀ (Latimer)*	.600	13.40	10.80	-	.0500	.1400	-
Brown leghorn ♂	1.500	26.50	17.70	1.45	-	.1200	-
Brown leghorn ♀	1.580	16.70	18.20	2.28	-	.1610	-

*Calculated on net body weight.

ported for chickens by Mayhew and Upp[7] which is similar to the type reported for mice in that it is inherited as a Mendelian recessive. These birds can be distinguished from bantams by certain anatomical differences such as degenerate sex organs. Landauer[4] states that this dwarf condition is associated with a thyroid deficiency suggesting cretinism. Unfortunately, no mention was made of the pituitary glands of these animals.

By studies of crosses between bantams and larger breeds of fowl, Punnett and Bailey[8] suggested that the inheritance of weight in poultry involves several factors which are capable of segregating during gametogemesis. Blunn and Gregory[1] have shown that there is an embryological basis of size inheritance from their comparison of the embryos of white leghorns and Rhode Island Reds which are distinctly different breeds on the basis of size. The embryos of the heavier breed (Rhode Island Reds), during the incubation period, had more cells per unit volume, even though the weights of the embryos of both types were similar. Thus at least two types of dwarfism occur in poultry based on a genetical classification. No attempt is made to explain the dwarf condition of the bantams on an endocrine basis even though there is a difference in weight in certain of the endocrine glands.

Summary

1. The endocrine weights of adult male and female bantams are presented together with the weights calculated on the basis of 100 grams body weight.

2. Comparisons of the weights of the thyroid, hypophysis and adrenals of the bantams and white leghorns on the basis of equal body weight, show that the hypophysis in the bantams is heavier, the thyroid is lighter, but that the adrenals are approximately the same in both groups of birds.

3. No sex differences are noted in the endocrine weights of the bantam fowl when calculated as a per cent of body weight.

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RELATIONSHIP BETWEEN THE FIRST CLEAVAGE SPINDLE AND MOSAIC FORMATION

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GYNANDROMORPHS and their production, in nature or by the use of X-rays, has been the subject of much discussion. Patterson's "Mechanism of Mosaics"[14] indicates proof of the "elimination of the *X* chromosome theory." In two papers, Patterson[13,14], suggests the possibility of a relationship between the first cleavage spindle and the future type of gynandromorph, also the rôle played by the cytoplasm, whether affected by the X-ray or in its natural state. Other writers have hinted at this relationship but none has directly pointed out the above possibilities. This is perhaps due to the fact that gynandromorph material was hard to obtain until Patterson devised the X-ray method.

In Patterson's data there are differentiated eight classes of gynandromorphs. The basic cause for the production of these types can be explained by the elimination of the *X* chromosome either by X-ray or by natural phenomena; however, this does not explain why the same set of conditions produces separate classes of gynandromorphs.

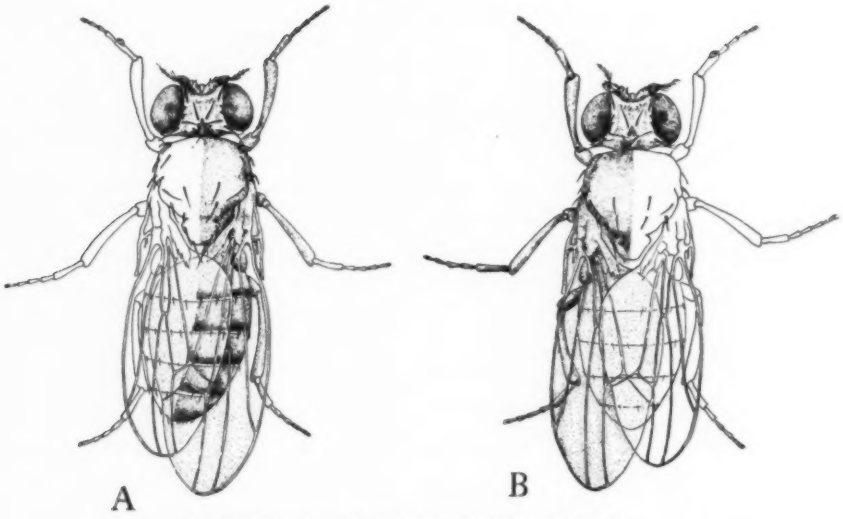
The above problem can be outlined as follows: (1) At what angle does the first cleavage spindle ordinarily lie? (2) What deviation of the first cleavage spindle from this angle may exist? (3) What relation is there between the direction of the spindle and the various classes of gynandromorphs? (4) What is the relation of nuclear patterns to the various cleavage classes above mentioned? (5) What rôle may the cytoplasm play in the determination of the type of character of the future gynandromorph?

From the literature dealing with dipteran embryology it is noted that Weismann[17] considered only the external differentiation and Noach[11], Blochman[1], and Henking[3], the gross embryological processes. The later insect embryologists, Tanquary[16], Nelson[10], and Huettner[5], have hinted at the possibilities of the meaning of the various cleavage patterns found in the developing egg, but all of them assumed that there was one set type, and that uniform to the whole order, so ignored the question. This literature, in giving methods of fixation and ways of handling the eggs, was of immense value in this work.

Acknowledgment is due to Dr. J. T. Patterson for suggesting this problem, for the use of his data, and for personal supervision of the problem, and to Dr. D. B. Casteel for his encouragement and advice.

Promorphology of the Drosophilan Egg

Ovaries from females three or four days old were fixed either by Carnoy's method or by the hot Kahle method. Sections were made of individual ova and of complete ovaries. It was observed that there is evidence of an existing bilaterally in the ovarian egg—that a line passes from a point just behind the micropyle to the posterior end of the egg which will correspond, more or less, with the longitudinal axis of the future embryo; that this also corresponds more or less with the longitudinal axis of the mother; that the ovarian egg likewise shows anterior-posterior differentiation of cytoplasm; and that in longitudinal section it can be observed that the right and left sides of the cortical öoplasm are the same and correspond to the right and left sides of the resultant embryo. It is shown that the ventral plate is the



COMMON GYNANDROMORPHIC TYPES

Figure 10

A—A gynandromorphic fly (No. 192) from an X-rayed wild-type male mated to a yellow scute female. The shaded area indicates the female tissue. Note that this animal is a "near bilateral individual"; however it is to be observed that female tissue passes over the median dividing line, and that the head is entirely female. Thus the animal cannot be considered to be strictly a bilateral individual. Stock from Patterson. *B*—A gynandromorphic fly (No. 284a) from an X-rayed apricot male mated to a yellow scute[4] female. The shaded area indicates the female tissue. Note that only the upper left quadrant is female; this, however, includes the wing. The rest of the body is male and the head is female, thus producing an animal falling in the one-quarter—three-quarter class. Stock from Patterson.

first part of the blastoderm to develop. That this is true in Drosophila is substantiated by 150 slides, prepared in this study, which show that differentiation begins with the anterior part of the ventral plate. Then transverse and sagittal sections should show definite areas of öoplasm. Hence, it was postulated that if there exists a definite promorphology of the ovarian egg, then the ventral part of the öoplasm and the ventral lateral sides should appear to be thicker than the dorsal lateral and posterior sides. An attempt to prove this was made, but out of fifty slides only three showed orientation in such a way as to substantiate the above statement.

Classification of First Cleavage Angles

Patterson and others following the theory of the elimination of a whole or a part of the X-chromosome in the production of gynandromorphs, have advanced the hypothesis that the elimination should in most cases occur in the first cleavage spindle. The angle at which the spindle lies with reference to the longitudinal axis of the egg would indicate the type of gynandromorph it will produce. This idea was advanced by Morgan who considered that the varying positions of the cleavage angles would explain the various classes of gynandromorphs. This, however, is inadequate to explain the composition of some of Patterson's mosaics, which are decidedly mixed so far as genetically diverse tissue is concerned. It would seem probable that Morgan thought that the directions of the first cleavage spindle determined the distribution of nuclei later produced. Patterson has suggested that the following factors are responsible for the dis-

tribution of nuclei: first, a combination of the angle of the first cleavage spindle and the promorphology of the egg; second, the effect of the cytoplasm; third, the direction which the other cleavage spindles take with reference to the sides of the egg and with each other.

With this in mind, eggs falling within "the half hour limit" (Huettner[5]) were carefully examined for the presence of the first cleavage spindle. Six of these were found and assigned to four classes. These classes are illustrated at the top of Figure 11 *A-D*. These type illustrations were obtained by projecting, with a camera lucida, the image of an egg showing two nuclei or the first division spindles. A line was then drawn from a point just behind the mircropyle to the posterior end of the egg. This line divides the egg into its lateral parts. The angle to the right and left of this line was determined by the use of a protractor.

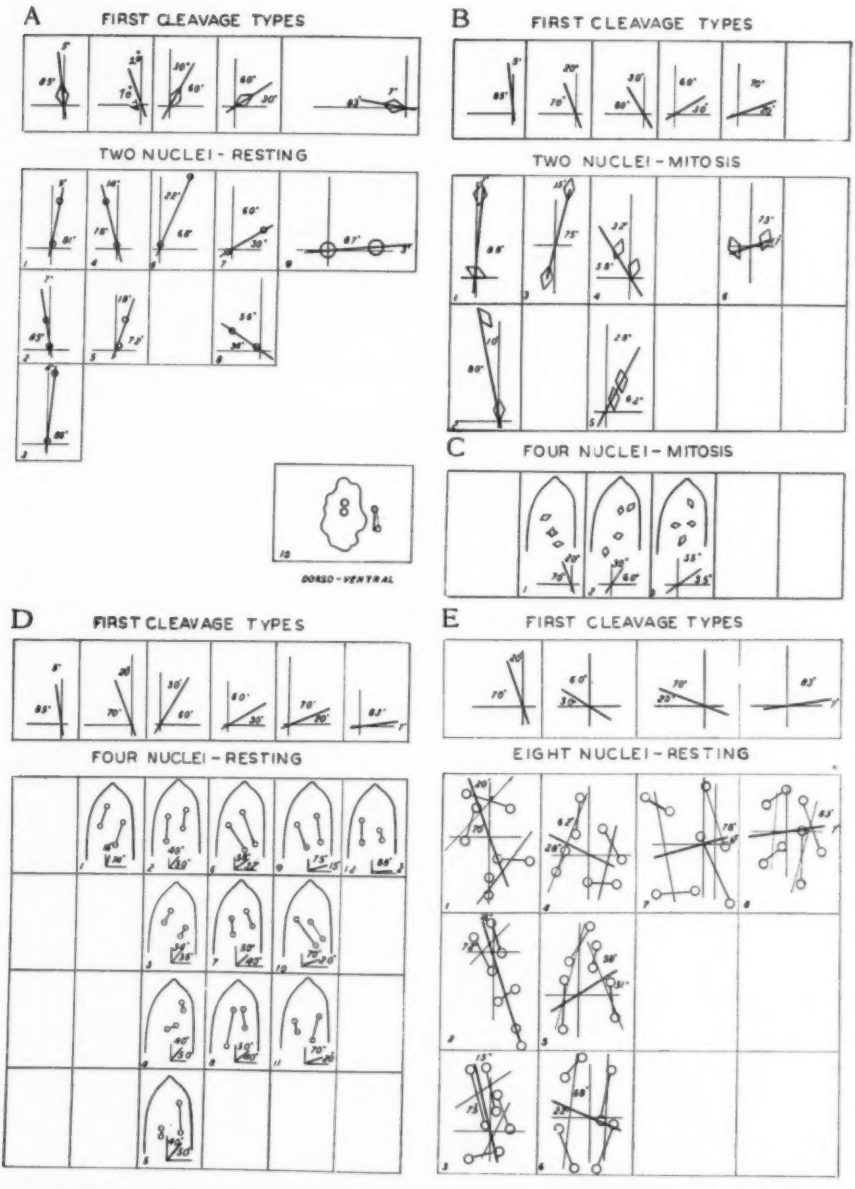
A method was now to be sought for by which the sequent cleavages might be classified on the basis of like angles. When four nuclei are present they usually lie at different levels in the cytoplasm and when there are two or more spindles their axes may run in quite different directions. Since camera lucida drawings are in one plane and do not satisfactorily represent these relationships, it was found necessary to make models of the nuclei from which a three dimensional picture could be obtained.

Granting that a longitudinal axis can be determined as a promorphological feature of the egg, then a plane perpendicular to this axis can be passed through this three-dimensional model. In the early stages the nuclei falling on the one side or the other of a longitudinal plane may be said to be the ancestors of that side. The value of this statement will be taken up in the discussion.

The projection images from forty-five slides were accurately measured. The distances apart of the nuclei, both in vertical and horizontal planes, were recorded in micra. After these measurements were checked for accuracy they were transferred to plates of glass, each of which represented a thickness of 7μ. The total number of plates represented an egg as viewed from the dorsal surface. From this a model was constructed using beads to represent the nuclei and rods to represent the distance between the nuclei. These models are pictured on Figure 12 *A-C* opposite the dorsal tracings.

By the use of the dorsal tracings and the model constructed from them, it would seem evident that two cells or spindles lying in the same plane should be descended from a previous nucleus lying in that plane. To substantiate this supposition the first cleavage spindle and several subsequent cleavage spindles were measured. The measurements ranged from 17μ at metaphase to 30μ at telophase. By applying this directional principle to the models we have a guide in the tracing of cell lineage. To illustrate the workings of this guide to cell lineage the line of descent is thus traced from the nuclear stage back to the first cleavage spindle. The positions of the nuclei during the nuclear stage are measured in both the longitudinal and vertical planes, both for distance apart and angular divergence from the axis, delineated on Figure 11 *C2f*. Referring to Figure 11 *C2e*, which represents the position of a four nuclear stage in mitosis, it is seen that this change from the nuclear stage to the four nuclei in mitosis comes about by reducing the resting nuclei of the eight nuclear stage to the dividing four nuclei from which they arose.

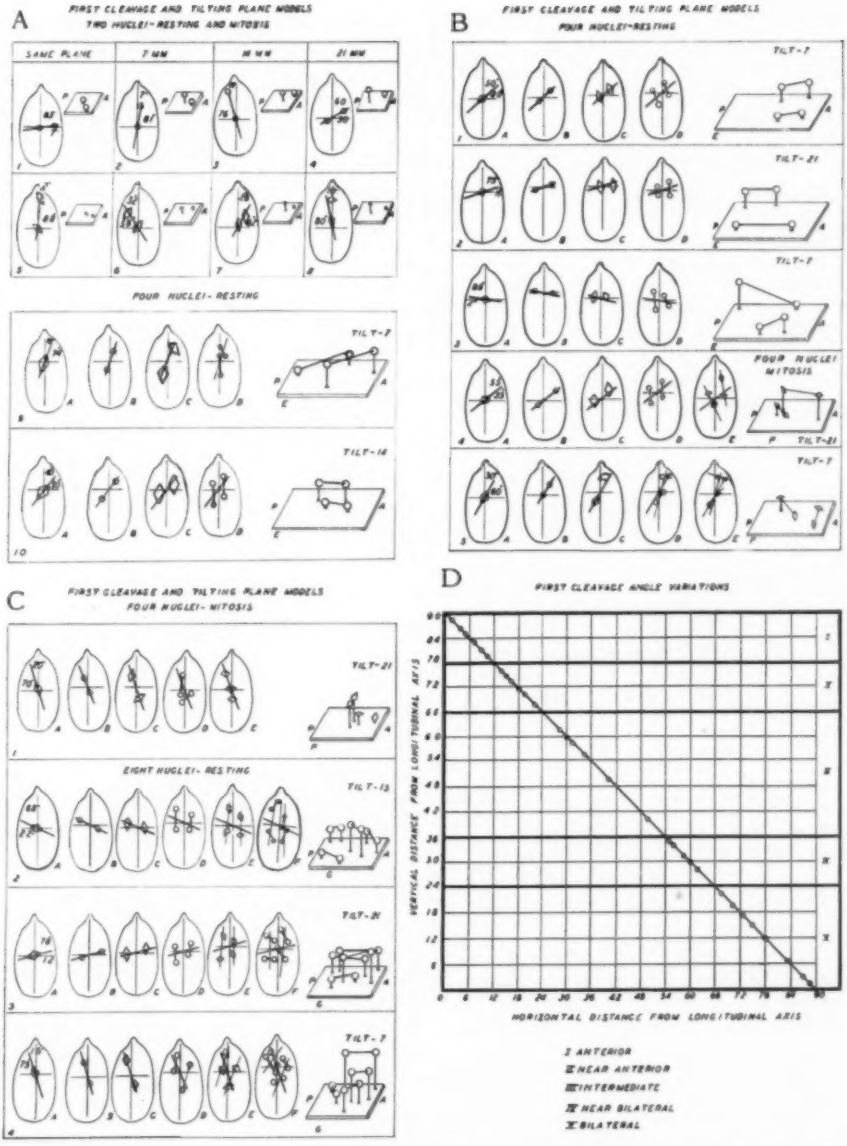
It is assumed that the median point of the individual four nuclear spindles represents the location of the "parent" resting nucleus of the four stage. The reduction of the four-nucleus resting stage to the two-nucleus mitotic stage occurs by the process given. However, a tilting takes place brought about by the fact that a change of angular distance occurs when mitotic spindles are reduced to the two-nucleus resting stage. A line drawn connecting the two resting nuclei is then the direction of tilt of the first cleavage spindle from which the eight-nucleus stage originated. The majority of the



TRACING CELL LINEAGE IN THE CLEAVING DROSOPHILA EGG

Figure 11

Note: At the top of each section on this plate is found a classification of first cleavage spindle angles, showing the angle that the spindle takes with the axis of the egg. *A-B*—A classification of traced first cleavage spindle angles from the two nuclei stage. *A10* shows the only dorsal-ventral type found. *C*—The tracing of four-nuclei resting stages and (*D*) of corresponding mitotic stages, back to a theoretical position for the first cleavage spindle. *E*—Similar theoretical reconstruction of the lineage of eight-nuclei stages.



MODELS USED IN TRACING CELL LINEAGE AND THE METHOD OF TRACING

Figure 12

A—Illustrations of the various positions of the cleavage spindles found. *B-C*—Tracing the tilting planes of various four nuclei stages. Tilt 21 indicates a spindle whose axis is 21 mu. from the horizontal. *D*—A graphic line up of actual first cleavage spindles and of traced spindles to show that the position of the first cleavage spindle is purely a matter of chance.

traced first cleavage spindles arrange themselves into classes that were actually observed (see Figure 11*A-D*). However, it was found necessary to erect some intermediate classes between 5°-85°, 30°-60°, 60°-30°, and 85°-5°.

On examination of actual first cleavage spindles and of these traced, it was found that while the traced first cleavage spindles followed the same classification as the actual ones, there had been tilting from the horizontal plane. This tilting, however, ranges from zero to a tilt of 21μ. This method of recording the tilting was to use the distance from the first recorded nucleus to the last recorded.

Shifting of the nuclei, in general, is not noticed until the four-nucleus stage is reached (Figure 11 *D*). Here the future basis for the scattering of genetically diverse tissue may be first initiated.

The tracing of the first cleavage, types of shifting of the nuclei, and tilts of cleavage angles were made for the various slides and recorded on Figure 11 and Figure 12 *A-C*.

Discussion

In a study of these data an attempt was made to show that the egg possesses a definite promorphology, consisting of a differentiation of the egg anteriorly, posteriorly, and laterally, as well as a seeming thickening of the cytoplasm on the ventral surface as compared with that of the dorsal surface. Also a plane can be passed through a point just behind the micropyle dividing the egg bilaterally.

Morgan in his *Experimental Embryology* uses the Drosophila egg as an example of bilaterality among insect eggs. He says:

> Eggs of many insects have a marked bilateral form which in a way corresponds with that of the mother's body. The anterior end of the insect's egg is not the point of the surface at which the polar bodies are given off. These lie anteriorly but on the dorsal side of the egg at a point generally not very far from the micropyle of the egg through which the sperm enters. The plane of bilaterality of the embryo corresponds with that of the egg. The cleavage of the insect egg is centrolecithal, that is, the segmentation nuclei divides first into two nuclei, and the daughter nuclei later divide again and again, but the protoplasm of the surface of the egg does not split up at this time, only when a large number of nuclei have appeared and have reached the surface does this layer of protoplasm that covers the egg become constricted around these nuclei into a large number of cells. The bilaterality of the embryo proper can become apparent only when the embryonic organs develop out of this surface layer.

Patterson, Morgan and others have postulated the idea that the promorphology of the embryo is responsible for its bilaterality. This promorphology is purely maternal.

Patterson has pointed out the development of the parthenogenic egg as a proof, not easily shaken, of essential bilaterality; that is, the genes responsible for the production of the egg are both maternal and paternal, deriving from the parents of the female laying the egg. Since in parthenogenesis there is no fertilization and the egg nevertheless undergoes cleavage and develops into a bilateral animal, the only available factors for the production of any bilateral or other feature of the egg are female. Thus the female Drosophila must receive genes from her mother and father which presumably are carried in the homozygous state. From this we can say that a Drosophila egg is a Drosophila egg due to the fact that the only genes present are those for production of a Drosophila egg. The same argument will hold true that only a Drosophila embryo could develop from a Drosophila egg. Loeb[7] says that the egg is the embryo in the rough, the cleavage cells are literally the refiners and decorators as to form and character. This, of course, must be taken figuratively due to the fact that genic material must be present to cause the progressive chiselling out of the embryo.

Conklin's[2] more modern statement of cytoplasmic inheritance is more explicit than Loeb's[7]. It consists of the following:

> There is no doubt that most of the differentiation of the egg cytoplasm has arisen during the ovarian history of the egg and as a result of the interaction of the nucleus and cytoplasm, the fact remains that at the time

of fertilization the hereditary potencies of the two germ cells are not equal. All the early stages of development, including the polarity, symmetry type of cleavage, the pattern or relative position, and proportion of future organs being foreshadowed in the cytoplasm of the egg cell, while only the differentiation of later development are fixed by the sperm. In short, the egg cytoplasm fixes the general type of development and the sperm and the egg nucleus supply only the details. If, as implied, the egg nucleus at first has already produced its effects on the cytoplasm, it has done something more than supply the details, and as to the sperm nucleus, I should substitute nearly all the stages of development later than the gastrula. Moreover, sex is certainly one of the fundamental characters of the organism, yet it appears to be determined at fertilization by the chromosomal combination formed at that time.

Morgan comments on the above statement and says:

That since the cytoplasm of the egg has been under the influence of its new nucleus with a paternal and maternal group of chromosomes there is no direct means of determining whether its characteristics are due to such an influence or has always been free from it.

Pauli[12] attempted to prove that the embryo was foreshadowed in the cytoplasm of the egg. Her conclusions are well in harmony with Conklin's and they are:

As the results of my experiments it can be concluded that the embryos of *Calliphora erythorcephia* and *Musca domestica* are preformed in the blastoderm.

While there is but meager evidence for the thickening of the ventral ooplasm in the ovarian egg there seems to be good reasons for its being so. In the work herein recorded, it is found that the ventral plate is formed near the anterior end, just prior to the time that the pole cells are pushed out posteriorly. The dorsal side follows this shortly. This, in fact, was observed by Huettner[5] as he saw the blastoderm nuclei migrate out to the cortical ooplasm in unison while posteriorly the pole-cells were extruded. Nelson[10] says:

It should, however, be always borne in mind that these processes do not take place simultaneously over the entire surface of the egg, or even any extended part of it. They commence where the cleavage cells first reach the cortical layer, namely, on the ventral side near the anterior end, then extend rapidly over the entire anterior third of the egg, thence progressing slowly caudad, so that all phases of the process of blastoderm formation may frequently be observed in a single egg. (Page 29.)

On pages 31-32 Nelson states:

The blastoderm is not of uniform thickness throughout, but is thinner on the dorsal than on the ventral side. It is evidenced that the blastoderm forming cells of posterior region are much less numerous than those of the anterior region—in trifle older stages the difference in thicknesses between the dorsal and ventral blastoderm is more marked. Moreover, the thicker blastoderm of the ventral side is continued over the anterior pole, being at this point even thicker than the ventral blastoderm itself.

The evidence here quoted is sufficient with few exceptions to become a part of the foundation of the rest of this discussion.

From Patterson's gynandromorph data eight possible classes were set up. See Table I. The largest classes were (1) anterior-posterior, (2) less than a quarter of the body involved, and (3) nearly bilateral. The nearly bilateral classes will be considered first. If the tables of Patterson's gynandromorphs are examined, one will find that there are two classes of these, namely, those nearly bilateral and those of the ¾, ¼ pattern. The class of bilaterals are the largest, the quarter-of-the-body-involved next, and the anterior last. The quarter-of-the-body-involved group will not be considered here as they are nondiagnostic or else not due to X-ray.

The question of the angular relation of the first cleavage spindle to the various classes has been held to be one of importance. Morgan and Huettner

Table I. Classification of Gynandromorphs

	Male X-rayed			Female X-rayed			Control		Total
	♂+♀ broken	♂+♀ not	♂+♀ not	♂+♀ not	♂+♀ not	♂+♀ broken	♂+♀ not	♂+♀ not	
Anterior posterior	8	10	14	3			2	1	38
Mixed genitalia	4	1					1		6
3/4 anterior posterior	1	8		2				4	15
Less than 1/8	6	16	6	8	6	1+	4	1	48
Mixed		2	1						3
More than 1/8 mixed	2	7			1			2	12
Quadrant		4					1		5
3/4-1/4 bilateral	12	24	4	8	9	3	2	4	66
Mixed genitalia		3			1				4
Bilateral	20	15	1	5	7		4	3	55
1/4 dorso-ventral	1	2	1		2				6

* - or deletion; + =indeterminate

each suggests that the first cleavage angle would determine the type of individual. This supposes a determinate type of cleavage. Patterson pointed out that the occurrence of the mixing of genetically diverse tissue found in some of the gynandromorphs indicated that it could not be the first cleavage angle alone nor could it be a determinate type of cleavage that is decisive in the production of a gynandromorph. From the cytological evidence offered here the first cleavage spindle angle either is a result of the angle at which the sperm nucleus fused with the female pronucleus or else of a shifting that occurred after the two had fused. This is based on the finding that the first cleavage spindle has no predetermined position. In this material there are four nuclear resting stages which are very different in appearance yet trace readily to a near bilateral type or, as in some, to a near anterior-posterior spindle. There are also intermediate spindles of the oblique types (Figure 11 *D*). Other types of traced first cleavage spindles will be parallel to the horizontal plane and others will show a tilt of 7 to 21μ from this plane (Figure 12 *A-C*). One might expect with a tilt of 21μ or more, to find more dorsoventral types. Patterson found at least six quarter dorsoventral types (Table I). In this work only one dorsoventral first cleavage spindle was found (Figure 11*A10*). It appears that this form occurs much more rarely as compared with the others.

If all of the first cleavage spindles, actual and traced, are graphically represented, it will be noticed (Figure 12*D*) that there are five localized areas. Although the data are few they seem to indicate that these types are the most frequent first cleavage spindles. Hence, two are toward the anterior-posterior end and three toward the bilateral end. These areas are in reality variations all along the line showing that in wild stock, regardless of the direction of the first cleavage spindle, all Drosophila formed are still bilateral animals. However, this does not mean that half of the body is a direct descendant of one of the first two cleavage nuclei. Note Controls in Table I. That is, in the controls, all eight types of gynandromorphs arise by natural elimination of the whole or part of the *X*-chromosome. This is a proof of indeterminate nuclear cleavage. Indeterminate nuclear cleavage must presuppose nuclear shifting. The shifting begins during the four-nuclear stage. Referring to Figure 11*D* it will be observed that near bilateral forms are represented by 11*D 2, 7, 11, 12,* anterior-posterior by types such as 11*D 5, 4, 10.* Evidence for the other types such as quadrants and dorsoventral forms may be obtained from the same data, due to the fact that there is no method by which we can determine future direction of nuclear migration.

Three drawings of the eight-nuclear stages are given on Figure 12*E*. The first is strictly bilateral, the next, one cell out of place, and the last, two cells out of place. From these types of shifting, one may pass naturally to the nearly bilateral or the more than bilateral forms. If the symbols for yellow and grey are placed in the two-nuclear stage of any of the pictured eight-nuclear drawings, then more than bilateral or less than bilateral forms could result. Recently two other workers, Sturtevant[15] and Whiting[18], have both recognized the above possibility in part. Sturtevant says in his article, Page 337:

> There is no available information as to the pattern of cleavage in Drosophila or in any related insect, though it appears probable that the early divisions are not oriented in a fixed fashion or pattern, so that the cells in a given part of the blastoderm have no constant genetic relationship to those in any other given part. This, however, is only a surmise.

Page 352:

> The gynandromorphs described in this paper and the earlier ones described for Drosophila by Morgan and Bridges and others make it quite clear that the cleavage of the egg is indeterminate. There is no definite pattern among mosaics which can only mean that the cleavage nuclei are disturbed to the blastoderm differently in different embryos. It follows that there are no potential differences among the nuclei before they migrate to the surface of the egg.

Again on Page 352 he states:

> There remain two ways of interpreting the results. There may be cytoplasmic differentiation, or the different portions of the blastoderm, may be functions of their position. There is no evidence at present to show this true for the embryo.

The statement of Sturtevant that it appears probable that the early divisions are not created in a fixed fashion or pattern, must be augmented by saying that there is much evidence that the majority of early cleavage patterns are essentially bilateral to the longitudinal axis. Still it must be held in mind that there are grounds to believe that mixing of genetically diverse tissue occurs due to the shifting of the nuclei.

The above statement does not mean that a set pattern is found. It merely implies that regardless of the pattern, bilaterality is still more or less maintained. Hence, to explain the anterior-posterior and the small dorsal-ventral classes, it must be remembered that, even though the external markings are anterior-posterior or dorso-ventral, the fly is still a bilateral animal. This would then imply that the nuclei which produced the diverse markings shifted in the direction in which the markings are found on the adult fly, yet at the same time kept the same near bilateral relationship either to the median or the tilted plane. Those nuclei lying in a plane greatly tilted away from the axis would, of course, possess in part dorso-ventral markings.

What then is the cause of nuclear shifting? Nelson[10] says:

> That further movement of the nuclei after telophase is contrary to the known biological laws, that is the nuclei in the resting stage cannot assume an amoeboid form and crawl about as they seem to do. Diehl has proven in the honeybee that the movement is due to cytoplasmic streaming. Thus the nuclei are carried along with this streaming.

It is to be remembered that, in these earlier stages, the islands of protoplasm are limited, and thus shifting should be more pronounced as the number of cleavage cells increase. Hence, shifting of nuclei should be proportional to the number of cleavage cells present, which in turn is dependent on the number of cytoplasmic islands present. It then seems to follow that when shifting does occur in later stages that it must occur in its own immediate region, i. e., the anterior, medial, or posterior.

Cytoplasmic streaming, which causes the apparent nuclear shifting, may be due to the changes in surface tension present at the time, when two nuclei are entering into the resting stage. This would imply that since all nuclei present in the egg divide in unison, the sum of the collective movements due to changes in surface tension produce cytoplasmic movement.

Comparing the gynandromorph data from the X-rayed material with that of the controls, it is concluded that there is probably no specific difference. See Table I. The only observable effect is an increase in rate of production of the various types. Of course, more breakage is apparent but the relative rates are the same.

The only effect which might be cytoplasmic other than nuclear shifting is the high rate of loss of either *X*, maternal or paternal.

Often it could not be determined whether the *X* was broken or entirely absent in some of the gnandromorphs resulting from X-rayed males. This might account for some of the apparent discrepancies in proportion of X-chromosomes of paternal or maternal origin lost in X-rayed males and females See Table I.

Conclusions

1. There is no definite angle of the first cleavage spindle. Then, given a normal wild stock whose chromosomes have no other genes present than those for normal, regardless of which angle the first cleavage spindle makes with the longitudinal axis of the embryo, a bilateral individual will result from the ensuing cleavages.

2. From cytological evidence offered here the deviations of the first cleavage

spindle angles are due to the fusion between the sperm pronucleus and the female pronucleus and to the shifting which may subsequently occur.

3. No definite relationships exist between the direction of the first cleavage spindle and the various classes of gynandromorphs. On the examination of gynandromorphs and mosaics, it becomes apparent that the bilateral sides are not necessarily direct descendants of the two cells resulting from the first cleavage.

4. There are several types of nuclear shifting in the bilateral and tilted plane, that is anterior-posterior, three-quarters-one-quarter anterior-posterior, three-quarters-one-quarter bilateral, and bilateral. Most of the distribution of genetically diverse tissue of mosaics can be explained on the grounds of nuclear shifting.

5. Since nuclear shifting is the chief factor in the determination of the type of gynandromorphs produced, then cytoplasmic streaming which is connected with nuclear shifting plays an important rôle in the determination of gynandromorphs.

6. Drosophila eggs have a definite promorphology such as bilaterality, symmetry, and polarization. This is to be attributed to genes coming from the maternal and paternal side of the female producing the egg.

7. Bilaterality of the individual is a function of the egg.

8. The cleavage of the egg of *Drosophila melanogaster* is of the indeterminate type.

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P	?	brown, pink eyed short eared dilute	aabbppsed/sed	low	excellent	.75	1.00	1.25	1.75
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Ml	40+	leaden	aabbCCDDll	low	excellent	.75	1.00	1.25	1.75
M		Brown, pink eye short ear, leaden	aabbppsesell	low	excellent	.50	.75	1.00	1.50
E		Pink eye extreme dilute Shaker 1	AABB pcdsh1/pcdsh1	low	excellent	.75	1.00	1.25	1.75
W	?	Shaker 2 wavy 2	$sh_2sh_2w_2w_2$	low	excellent	.75	1.00	1.25	1.75
V	?	piebald, wavy 1 leaden waltzing	ssw_1w_1llvv	low	excellent	.75	1.00	1.25	1.75
AW	12+	white bellied black agouti	AwAwBBCCDD	excellent	good	.50	.75	1.00	1.50

†D = Animals 4-5 weeks old; E = Animals 4-5 months old.

For order blanks and additional information regarding the suitability of these strains for specific research problems, write to:

ROSCOE B. JACKSON MEMORIAL LABORATORY

SUPPLY DEPARTMENT

Bar Harbor **Maine**